CYTOTAXONOMIC STUDIES IN THE SECTION ANNUI OF *SENECIO*

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ABSTRACT

Senecio squalidus, a Mediterranean endemic, became established in Britain about 180 years ago, where it is now common and widespread.

S. squalidus is represented in Sicily by two distinct taxa: the lowland S. chrysanthemifolius, and the montane S. aetnensis. On the basis of their distinctiveness these taxa are retained as separate species. Where these two species meet they form hybrid swarms, and bipolar introgression occurs. The British S. squalidus is morphologically intermediate between the two Sicilian species, but its autonomy and circumscribed morphology indicate that it should be treated as a distinct species of hybrid origin.

In Britain, S. squalidus (2n = 20) hybridises with S. vulgaris and S. viscosus (both 2n = 40). Both triploid hybrids are very highly sterile.

A ligulate variety of S. vulgaris shows a close geographical and historical correlation with the spread of S. squalidus in Britain, and indicates introgression into S. vulgaris from S. squalidus. The rare occurrence of segregating fertile hybrid material supports this hypothesis.

Experiments show that introgression can occur via the rare seed set by the triploid F_1 S. squalidus X S. viscosus at the more or less pentaploid level (2n = 47 - 50). Subsequent generations from these pentaploids tend towards the tetraploid level and increasing fertility. This may be analogous to the method of introgression into S. vulgaris.

S. cambrensis, an allohexaploid (2n = 60) from *S. vulgaris* X *S. squalidus*, has arisen in Britain, probably within the last 50 years, and is still restricted to north Wales and Cheshire. This species is now segregating into ligulate and eligulate races.

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INTRODUCTION

THE GENUS SENECIO

Senecio is a large, widely spread, and diverse genus. Estimates of the numbers of species in the genus range from about 1000 to over 2000. These estimates are of little relevance until the complex synonymy of many of the species and the limits of the genus are determined. Additionally, reference to recent literature shows that considerable numbers of completely new species are still being described, especially from Central and South America (for example, the papers of A.L. Cabrera appearing in current issues of the Bol. Soc. Arg. Bot.; and of J. Cuatrecasas in the Ann. Miss. Bot. Gard.) and from Africa (G. Cufodontis in Senck. Biol.).

Taxonomic limits of the genus are open to a number of interpretations, and vary accordingly. Intrageneric divisions are similarly given different treatments, for example by de Candolle (1837), Fischer and Meyer (1841-2), Harvey and Sonder (1864-5), Hoffman (1897), Muschler (1909), Greenman (1915), and Kitamura (1939). Many of these treatments are of geographically restricted numbers of species. Revision of the whole genus, including the neighbouring taxa, is necessary, but the immensity of the task renders it impossible for a single investigator. Consequently, recent re-examinations of the systematics of Senecio and the Senecioneae have necessarily been based on a restricted number of characters. Thus, Drury and Watson

(1965, 1966) concentrated on trichomes, corolla venation, and ovarian crystals; and several workers have surveyed chromosome numbers (Afzelius, 1924, 1949, 1967; Ornduff et al, 1963, 1967; Palmblad, 1965; and Turner and Lewis, 1965).

CHROMOSOME EVOLUTION IN SENECIO

Evolution of the karyotype occurs in several ways. The phenomena of inter- and intra-chromosomal re-arrangements, and of loss and gain of complete chromosomes (as in aneuploidy, polysomy, and polyploidy) are well documented. In addition evolutionary changes in chromosome mass, and particularly in DNA content have recently been increasingly investigated as biochemical, biophysical, and microscopic techniques have improved.

Differences in chromosome size between various taxa of Senecio are apparent from the observations and published figures of many workers (for example: Afzelius, 1924, 1949; Goldsmith and Krupko, 1948; Palmblad, 1965; and Turner and Lewis, 1965). In particular, Marchant (1968) has constructed a possible phylogenetic sequence based on increases in chromosome size in succulent African Senecio species, all with the chromosome number of 2n = 20.

In general, the main evolutionary lines of the genus appear to be represented by species with smallish chromosomes of the order of size encountered in the British Annui. Large chromosomes, and very small chromosomes, as with high chromosome numbers may only occur in "evolutionary dead ends", such as in the African succulents, the African

"tree senecios", and the endemic Senecio species of the Canary Islands.

Reported chromosome numbers for the genus Senecio are given, on a geographical basis, in Table 1. The base number of the genus is generally accepted as being x = 5, this probably being the base number of the Senecioneae itself. The highest chromosome numbers given in the Table are probably the result of autopolyploidisation, and at such high chromosome numbers "a few genomes more or less are of little taxonomic or biological significance" (Afzelius, 1949).

The base number of x = 5 has been questioned by Ornduff et al (1963, 1967), who suggest that the base number is more probably x = 10. Their reasons are the rarity or absence of species with n = 15, 25, 35, etc.; the possibility of aneuploid reduction series existing (for example n = 30 to 19, and n = 12 to 9: see Table 1); and the fact that the species of Senecio and the closely related Emilia recorded as having n = 5 (Turner and Lewis, 1965) are all annuals. This corresponds with the observations of Stebbins (1950) and Grant (1958) that taxa at the lower end of such reduction series are frequently annual.

Turner and Lewis (1965) argue against Ornduff and his co-workers on the basis that although numbers of n = 5 and n = 10 are common in Africa, only one intermediate number has been recorded: n = 9 in S. arenarius Thunb., which is closely related to and sympatric with S. elegans L. (n = 10)

TABLE 1

Chromosome numbers of Senecio species, and their World distributions

(Records are of described species for which definite chromosome numbers have been reported, bracketed numbers are for approximated counts)

NUMBERS OF SPECIES	haploid chromosome number																										
	5	9	10	12	15	16	18	19	20	22	23	24	25	28	30	38	40	45	46	48	50	65	69	70	80	90	TOTAL
Africa, south of Sahara	3	1	35 (1)		2				6 (1)						6		1				1			(1)		2	57 (3)
Canary Islands									(1)						5 (1)												5 (2)
Mediterranean Europe, North Africa, and Asia Minor			4						6 (1)						1												11 (1)
non-Mediterranean Europe			2			1			18 (1)			3 (1)	2		1 (1)		3	(2)		(1)	1						31 (6)
Asia, excluding Asia Minor			1 (1)	1			2	1	17	1	2	5 (2)			2	1	3	1									37 (3)
Australasia									6						1		1 (1)				1						9 (1)
Eurasian Arctic									(1)		1	1 (2)	2 (1)					(1)									4 (5)
American Arctic									1		1 (1)	3	1				(1)		2						(2)		8 (4)
North America									33	4 (1)	26 (1)	3	1	1			3	1 (1)	4 (1)				1			(1)	77 (5)
Central America									12		2				5			(1)				(1)					19 (2)
South America			1						15								3 (1)										19 (1)
TOTAL	3	1	43 (2)	1	2	1	2	1	114 (5)	5 (1)	32 (2)	15 (5)	6 (1)	1	21 (2)	1	14 (3)	2 (5)	6 (1)	(1)	3	(1)	1	(1)	(2)	2 (1)	277 (33)

ploidy level																										
	x = 5	x		2x		3x				4x				5x		6x		8x	9x			10x	13x		14x	16x	18x
	x = 23											x								2x				3x			
	x = 24/25												x								2x						

Notes on the derivation of Table 1:

Nomenclatural problems are manifest in the Senecioneae, but the majority of species whose chromosome numbers are recorded have apparently either been worked on directly by persons with a taxonomic interest in the group, or have had their status affirmed by such authorities. However, where applicable, certain adjustments have been made. Where a particular taxon is recorded by various authors by more than one specific name, the information for the purposes of Table 1 has been treated as applying to only one species. For example, reported chromosome counts of Senecio congestus (R.Br.) DC. and S. palustris (L.) Hook. are combined; as are S. integrifolius (L.) Clairv., S. spathulaefolius Gmel. and S. campestris (Retz.) DC..

Subspecific divisions are ignored, and in fact, in only six cases of the 23 recorded have taxonomic recognition been given to chromosome races within species by the authors.

Most of the species, although their geographical ranges may exceed the divisions given in the Table, have only had their chromosomes counted in a particular locality, and hence are only recorded for that division. Twelve species, mainly Arctic and Eurasian, have been counted in more than one division, and are recorded separately in the Table. Species known to have been recently introduced into new geographical divisions (for example the European S. jacobaea into America) are not included in this treatment.

A total, therefore, of nearly 300 of the 1000 - 2000 members of the genus have definite chromosome counts, with about another 30 provisional counts having been recorded. North American and European species are the best known cytologically. Polyploid chromosome races are known in 23 species; and aneuploid races have been recorded in 11 species, although some of these are probably erroneous counts. The polyploids show no particular frequencies in different sections of the genus. Aneuploids are common in the section Tephroseris (Schur.) Hoffm., where counts of n = 24 and 25, or n = 48 and 50 have been recorded in the same species. Afzelius (1949) suggested that this section has a base number of n = 25, with the occasional loss of a single chromosome.

The sources of the recorded chromosome numbers are listed overleaf. The majority of these references were traced directly or indirectly by using the chromosome number reviews of Maude (1939, 1940), Tischler (1950), Delay (1951), Darlington and Wylie (1955), Cave (1958 - 1964), and Love and Love (1961).

Notes on the derivation of Table 1 (continued):

The Table is drawn from the following published reports:

Afzelius (1924, 1949), Ali (1966), Arano (1960a, 1960b, 1962c),

Baker (1956), Banchetti (1961), Beaman and Turner (1962), Böcher and Larsen (1955), Borgmann (1964),

Chuang and Chao (1962), Covas and Huziker (1954), Covas and Schnack (1946, 1947), Diers (1961),

Favarger (1955), Hedberg (1967), Howard and 'E.A.E.' (1943), Johnston and Packer (1968),

King (1965), Kozuharoo and Kuzmanov (1964),

Larsen (1958, 1960a), Löve (1967), Löve and Löve (1956), Löve and Solbrig (1964), Lescova et al (1964),

Marchant (1968), Matsuura and Suto (1935), Mosquin and Hayley (1966), Mulligan (1959, 1961),

Nordenstam (1967a), Okabe (1931), Ornduff (1960, 1964), Ornduff et al (1965, 1967),

Packer (1964, 1968), Palmblad (1965), Powell and Turner (1963), Quezel (1955, 1957),

Rahn (1960), Reese (1952, 1957),

Schnack and Covas (1947), Snow (1959), Sokolovskaja (1960, 1963), Sokolovskaja and Strelkova (1938, 1940, 1960), Stoutamire and Beaman (1960), Sŭzuka and Koriba (1949),

Taylor and Brockman (1966), Turner and Lewis (1965), Turner et al (1961, 1962), Zhukova (1964, 1965a).

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of the Cape Province (Afzelius, 1949). They also suggest that selection would be strong against the triploid and pentaploid hybrids which might give rise to species with n = 15, 25, etc..

On the basis of chromosome numbers, the centre of origin of the genus was certainly in the Old World, since all but one of the recorded American and Australian species

have higher chromosome numbers of at least n = 20. If, indeed, x = 5 is the base number of the genus, then it probably originated in Africa rather than Asia.

Table 1 indicates (within the limits of data incorporating counts of less than 300 species from an estimated 1000 - 2000) that whatever the phylogenetic status of particular chromosome numbers, the bulk of geographical and evolutionary diversification at the species level has taken place at chromosome numbers of n = 10 and n = 20, the latter number particularly. In addition, a number of species and species groups both within Senecio and its related genera have evolved at about the n = 30 level.

It is possible that the Section Annui, on the basis of its centre of distribution (Mediterranean) and its chromosome numbers (many species, especially the perennials, have n = 10) is representative of the taxa from which n = 20 taxa developed and diversified.

Most of the African genera related to Senecio (see Table 2) also exhibit chromosome numbers based on 5, and probably at least some of these genera own a common origin with Senecio, or originated from Senecio itself. As with the African Senecio species, Emilia shows chromosome numbers of n = 5 and n = 10, and in this case there is little dispute that the polyploids are derivatives of the former (Ornduff et al, 1963).

The number n = 10 is particularly common in both Senecio and its related genera in Africa. The Senecio

Table 2 Reported chromosome numbers for genera of the Senecioneae s.l. (using the genera discussed by Ornduff et al, 1963 and 1967):

genus:	haploid chromosome number:	continental distribution:	alternative subfamilial classification:
Senecio	5, 9, 10, 15, 20, 30, 40, 50, (70), 90	Africa	
	10, 16, 20, 24, 25, 30, 40, (45), (48), 50	Europe	
	10, 12, 18, 19, 20, 22, 23, 24, 30, 38, 40, 50	Asia	
	20, 23, 24, 25, (40), (45), 46, (80)	Arctic	
	10, 20, 22, 23, 24, 25, 28, 30, 40, 45, 46, (65), 69, (90)	Americas	
Emilia	5, 10	Africa	
	10	Asia	
Gymnodiscus	9	Africa	
Cadiscus	10	Africa	Helenieae
Euryops	10	Africa	
Gamolepis	10	Africa	
Othonna	10	Africa	
Cassocephalum	10	Africa	
	20	Australasia	
Kleinia	10	Africa	
Cineraria	20	Africa	
Gynura	20	Africa	
	10	Australasia	
	10	Asia	
Arnica	38	Europe	Helenieae
	(20), 38	Asia	
	(28)	Arctic	
	19, (33), 38, (28), (47)	North America	
Doronicum	30, 60	Europe	
	30, 60	Asia	
Homogyne	(30), (34), (35)	Europe	

- continued -

Petasites	26, 29 2B, 30	Europe	
	29, 30	Asia	
	30	North America	
Tussilago	30	Europe	
Cacalia	20, 26, 30	Asia	
	25, 26, 27, 28, 30	N. & C. America	
Erechtites	20	Asia	
	20	North America	
Ligularia	(16), 24, 29, 30	Asia	
Mallotopus	9	Asia	Eupatorieae
Bedfordia	30	Australasia	
Brachyglottis	30	Australasia	
Arrhenechtites	(50)	Australasia	
Adenocaulon	23	N. & C. America	Mutisieae, Heliantheae, Inuleae
Crocidium	9	North America	Helenieae, Astereae
Dimeresia	7	North America	
Haploesthes	9, 18	North America	Helenieae, Astereae
Hulsea	19	North America	Helenieae
Lepidospartum	30, (45)	North America	Astereae
Luina	30	North America	
Psathyrotes	17, 19	North America	Helenieae
Tetradymia	30, 62	North America	
Whitneya	38	North America	Helenieae
Bartlettia	11	North America	
Pseudoclappia	(18)	North America	
Neurolaena	11	Central America	
Peucephyllum	20	Central America	Eupatorieae, Astereae
Schistocarpha	8	Central America	

- continued -

Werneria	50	Central America	
	(21), (50), (52), (53), (54), (75), (77), (103), (106)	South America	
Culcitium	20, 40	South America	
Liabum	(28)	South America	Heliantheae

Notes: The bracketed numbers are approximated counts.

The alternative taxonomic treatments of several of these genera are those of Bentham and Hooker (1873), and Hoffman (1897).

The Table is drawn from the following published reports in addition to those given in Table 1:

Arano (1962a, 1962b), Böcher and Larsen (1950), Borgmann (1964), Coleman (1965), Cooper (1936), De Jong and Longpré (1963),

Flövik (1940), Hagerup (1941), Hair and Beuzenberg (1959), Heiser (1963), Huziwara (1962),

Jorensen, Sorensen and Westeraard (1958), Langlet (1936), Lindqvist (1950), Löve (1966),

Maude (1940), Sakai (1934), Smith (1965), Sorensen and Christiansen (1964), Stebbins and Major (1965), Turner and Ellison (1960), Urbanska (1956), Zhukova (1965b, 1966).

Sections Leptophylli and Annui both exhibit this number, and the latter Section is common in the Mediterranean region, where it also exhibits chromosome numbers of n = 20, and overlaps geographically with Eurasian Sections of the genus (for example: Jacobaeae, Incani, and Fruticulosi) with n = 20. Several workers have placed species of the Annui in the Jacobaeae, possibly indicating an evolutionary continuity between the two Sections (see Table 3).

THE SECTION ANNUI

The species dealt with in detail in this thesis belong to the Section Annui of Senecio. The various interpretat--ions of the positions in the genus of the species involved are given in Table 3. In the wide sense in which I have used the name, the Annui consists of species with chromosome numbers of n = 5, 9, 10, 20, 30, 40, and 50 (see footnote) As much of the work in this thesis will deal with chromosome numbers of the British taxa, it is intended, in order to avoid tedious terminology, that the lowest haploid number of the European species, n = 10, will be referred to as the base number. Thus, the Section in Europe consists principally of diploid (2n = 20), and tetraploid (2n = 40) species.

Species types within the Annui are given in Table 4. The diploid species of the Annui are self-incompatible, with

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footnote: Although I have not had the opportunity to observe these n = 5 species, Afzelius (1924) placed one of them in the Annui.

Table 3 Different taxonomic treatments of species of the Annui (s. l.). (Names in capital letters are of Sections; others are of Sub-sections)

A = Hoffmann (1897)
B = Greenman (1915)
C = Harvey and Sonder (1894)
D = Dumortier (1827)
E = Boissier (1875)
F = Willkomm and Lange (1870)
G = Afzelius (1924, 1949, 1967)
H = Grenier and Godron (1850)
I = Muschler (1909)
K = De Candolle (1840)

	2n =	ANNUI	OBEJACOIDEAE	OBAEJACAE	ANNUI: Annui	ANNUI: Obejacoideae	ANNUI: Obaejacae	JACOBAEA	LEPTOPHYLLI	EUSENECIO	SPATHULATI	ERYTHRAEI
vulgaris L.	20	A B C	D	E F K			G			H		
sylvaticus L.	20	A B	D	E F K			G			H		
viscosus L.	20	A B	D	E F K			G			H		
lividus L.	20	A		E F K						H		
schimperi							G					
aegyptius L.	20			E K			G					
petraeus Boiss. et Reut.			F									
duriaei Gay.			F					K				
minutus DC.			F K									
glaucus L.			F K									
mohavensis Gray	20	B										
aphanactis Greene	20	B										
californicus DC.	20	B										
ampullaceus Hook.	20	B										
aetnensis Jan.	10		K			G						
squalidus L.	10		K			G		D				
gallicus Chaix.	10		F K			G		H				
nebrodensis L.	10		F			G		E A B K				
scandens Buch. Ham.	10				G							
decaisnei DC.				E K								
vernalis Waldst. et Kit.	10	A	K	E		G						
rodriguezii Willk.	10				G							
crassifolius Willk.	10		F K					H				
coronopifolius Desf.			K	E	G							
massaicus Maire	20				G							
pithosillum DC.		B										
dunensis								D				
elegans L.	10	B C			G							K
arenarius Th.	9	B C K			G							
maritimus L.		C										
littoreus Th.		C										
glutinosus Th.	10	C K			G							
leucanthemifolius Poir.	10		F K	E	G			H				
abrotanifolius L.	20							G K				
adonidifolius Lois.	20							G K F H D				
delphinifolius Vahl.	20		K		G			F				
inaequidens DC.	20								C K			
discifolius Oliv.	5				G						I	
hoggariensis Batt. et Trab.	30				G							

Table 4 Species types within the Annui s.l. (only species with recorded chromosome numbers are noted). S.I. = self-incompatible; S.C. = self-compatible

		DIPLOID		TETRAPLOID (or higher)
POLYCARPIC	S.I.	S. squalidus L. (Europe) including:	?	S. delphinifolius Vahl. (Mediterranean)
	S.I.	S. chrysanthemifolius Poir. (Italy and Sicily)	?	S. massaicus Maire (Morocco)
			?	S. adonidifolius Lois. (S.W. Europe)
	S.I.	S. aetnensis Ten. (Sicily)	?	S. abrotanifolius L. (Central Europe)
	S.I.	S. rodriguezii Willk. (Balearic Islands)	S.I.	S. inaequidens D.C. (S. Africa)
	?	S. leucanthemifolius Poir. (Mediterranean)	S.I.	S. lautus Forst. (Australia)
	S.I.	S. rupestris W.K. (S. Europe)	S.C.	S. lautus Sol. (New Zealand)
	S.I.	S. gallicus Chaix. (S.W. Europe)	S.C.	S. radiolatus F. Muell. 2n = 80 (New Zealand)
	?	S. arenarius Thunb. 2n = 18 (S. Africa)	S.C.	S. glaucophyllus Cheesem. 2n = 100 (New Zealand)
	?	S. elegans L. (S. Africa)	S.C.	S. sterquilinus Ornduff (New Zealand)
MONOCARPIC	S.I.	S. vernalis W.K. (Eurasia)	S.C.	S. aegyptius L. (Egypt)
			S.C.	S. lividus L. (Mediterranean)
			S.C.	S. sylvaticus L. (Eurasian)
			S.C.	S. vulgaris L. (Old World)
			S.C.	S. viscosus L. (Eurasian)
			?	S. ampullaceus Hook. (N. America)
			?	S. aphanactis Greene (N. America)
			?	S. mohavensis Gray (N. America)
			?	S. californicus D.C. (N. and Central America)

S. adonidifolius and S. abrotanifolius are closely related species usually placed in the Section Jacobaeae (see Table 3). In my opinion they resemble in some respects the polycarpic species of the Annui. Favarger (1965) mentions the possibility of races occuring of S. abrotanifolius with 2n = 20 as well as the reported 2n = 40 and 60. This would be a unique chromosome number amoung the Jacobaeae (usually 2n = 40), and suggests a link with the Annui. In addition, Drury and Watson (1965) on the basis of leaf morphology and types of trichomes, suggest that these two species are distinct from the Jacobaeae, although they do not suggest an alliance with the Annui.

conspicuous capitula, and are mainly polycarpic. They occur throughout the Old World, with the greatest diversity and number of species in the Mediterranean region. The tetraploids fall into two main categories: those resembling the diploids, except that they may be self-compatible; and monocarpic, exclusively self-compatible species with reduced floral parts. The former taxon is absent in the New World; the latter is Cosmopolitan, and due to Man's activities a few of its species have now become world-wide.

Two other taxa, one Australian, and one African show affinities with the polycarpic tetraploid Annui. Ornduff (1964) suggested that the Senecio lautus complex, endemic to Australia and New Zealand, does not owe its origin to South American material, thus probably placing its origin in the Old World. He also (R. Ornduff, personal communication, and 1964) reports that a sterile hybrid was obtained between S. lautus (Sol.) Ornduff and the introduced S. vulgaris L., which is a monocarpic tetraploid member of the Annui, and therefore one must assume, a fairly well advanced member of that Section. Herbarium specimens (BM and K) corresponding to Ornduff's species, and his photographs and descriptions (Ornduff, 1960) suggest that this taxon is at least closely related to the Annui. Mueller (1864) suggested an allegiance between S. lautus and S. vulgaris if the former "should prove annual". The chromosome numbers of the S. lautus complex are 2n = 40, 80, and 100. Both self-compatible and self-incompatible races are known in the 2n = 40 species, and the 2n = 80 and 100 species are

self-compatible, although they are probably usually outbreeding (Ornduff, 1960, 1962, and 1964; and Ali, 1966). The self-compatible races of S. lautus are apparently restricted to New Zealand, and this may indicate their derivation from the self-incompatible races of Australia (Ali, 1966).

The African S. inaequidens DC. may also be very closely related to the Annui, although Harvey and Sonder (1894) placed the species in the Leptophylli. This is a perennial South African species with 2n = 40; it is self-incompatible; and it is hybridisable with S. vulgaris (Harland, 1955). The species is often confused with S. lautus, and presents a variable range of similar morphology to that species (Lousley, 1961). Both S. lautus and S. inaequidens have been recorded as aliens in Britain (see Appendix Table 7) - probably as a result of introduction of seed in wool shoddy.

Hexaploids (2n = 60) have been recorded three times in the Annui: the allohexaploid S. cambrensis Rosser, which is discussed in detail later in the thesis; the annual, succulent, Saharan endemic S. hoggariensis Batt. et Trab. with n = 30 (Afzelius, 1967); and an unsubstantiated count of 2n = 60 for S. abrotanifolius var. tiroliensis Kerner in Western Europe (Mattick, in Tischler, 1950; and disputed by Favarger, 1965).

In general, the polycarpic diploid (2n = 20) species are taxonomically difficult. For example, the British

S. squalidus forms fertile hybrids and is difficult to distinguish at overlapping parts of their morphological ranges with both the Rumanian S. rupestris W. et K. (Walters, 1963), and the French S. gallicus Chaix. (Harland, 1955). These conditions prompted both authors to suggest that they were dealing with a single taxon. In addition, species which may appear to be well separated can be capable of forming fertile hybrids. For example: S. rodriguezii Willk., a maritime, Balearic Island species with a trailing habit, fleshy, greyish leaves, and small, purple ligules forms fertile hybrids in cultivation with the British S. squalidus L. (my own observations; and S.M. Walters, personal communication). Hybrids within the polycarpic diploids are given in Table 5.

The polycarpic tetraploid species are somewhat easier to distinguish, but confusion can still occur between species of such widely different geographic origins as those of S. lautus and S. inaequidens, as already discussed. In New Zealand (Ornduff, 1960, 1962, and 1964) and Australia (Ali, 1964a, 1964b, and 1966) the polymorphic nature of the S. lautus complex has been demonstrated. The Old World members of the polycarpic tetraploid Annui, however, appear to present relatively little difficulty taxonomically.

The monocarpic tetraploids are the only group in which all species are fairly distinct from one another. Thus, in Eurasia, S. lividus L., S. duriaei J. Gay, S. aegyptius L., S. vulgaris L., S. sylvaticus L., and S. viscosus L.

Table 5 Hybrids between species of the same chromosome number in Senecio Section Annui:

Reported hybrid:	Source:	Comments:
DIPLOIDS (2n = 20):		
S. gallicus Chaix. X S. squalidus L.	Harland (1955)	all experimentally produced, the F_1 hybrids being fertile
S. rupestris W.& K. X S. squalidus L.	Walters (1963)	
S. rodriguezii Willk. X S. squalidus L.	S.M. Walters (personal communication), and my own observations	
S. chrysanthemifolius Poir. X S. aetnensis Jan. (= S. X incisus Presl.)	my own observations (see pp. 36-65).	hybrid swarms are formed, and bipolar introgression takes place in Sicily where these two taxa of S. squalidus sensu lato meet
TETRAPLOIDS (2n = 40):		
S. inaequidens DC. X S. vulgaris L.	Harland (1955)	experimentally produced, no further details
S. lautus Sol. X S. vulgaris L.	R. Ornduff (personal communication; and Ornduff, 1964)	experimentally produced, hybrid vigorous, but sterile
S. lividus L. X S. vulgaris L. (S. X marceris Sennen)	specimen in BM from Spain, 1916	possibly BM specimen is correct, plant has intermediate characters, and has set seed
S. viscosus L. X S. vulgaris L. and S. sylvaticus L. X S. vulgaris L.	both hybrids have been reported from Sweden (Lindman, 1926; and Hylander, 1955). The former hybrid has been recorded in Britain by Riddelsdell (1923), Lousley (1944), and the BSBI Year Book for 1949	the herbarium specimens offer little evidence as to their parentage. Other possibilies are segregants of S. X londinensis or of S. X Viscidulus
S. viscosus L. X S. sylvaticus L. (= S. X viscidulus Scheele)	specimens are in most large herbaria; see also Lousley (1954)	a quite common hybrid which appears in many cases to be slightly fertile

are all "good species". Hybrids between members of this group have been recorded (see Table 5), but in contrast to the hybrids of the polycarpic diploid species, a considerable degree of sterility is apparent.

It is a reasonable assumption that the tetraploid taxa originated from the diploids. In addition to their chromosome numbers the tetraploids show other characters which are often regarded as indicating an evolutionarily derived condition. For example, they are often self-compatible, they occupy a wider range than do the diploids, and morphologically they are distinct from neighbouring Sections of the genus, - unlike the diploids. This correlates with the observations of Stebbins (1957), who quotes several examples where cross-fertilised taxa are considered to be ancestral to self-fertilised ones.

The polycarpic tetraploids closely resemble the polycarpic diploids. In this sense a similar relationship is indicated to that within Dactylis, Crepis, Paeonia, and other genera (Stebbins, 1950; Stebbins and Zohary, 1959), where morphologically and geographically separated diploid species are sympatric with a superstructure of taxonomically complex ploypoid species, whose morphological range does not exceed that of the diploid taxon as a whole. Stebbins (1966) suggests that the failure of such polyploids to evolve new characters is probably due to the retardation of evolutionary progress resulting from the presence of duplicated ancestral gene loci. This type of argument is

common where polyploidy is under consideration, and can be criticised on its central feature, - namely that only the rate of evolutionary change is slowed, and not its extent. Unless few sexual cycles are involved, this reduction in the rate of recombination is of little relevance. Where many generations are involved, selective pressures will be as responsible for the maintenance of polyploid gene pools as they are those of the diploids. As the species have similar environmental distributions, the same selective pressures are active against both diploids and polyploids, and hence, in relatively stable habitats phylogenetically related diploids and polyploids will tend to retain similar phenotypes. Of course, the potential heterozygosity inherent in polyploids may support a degree of plasticity in their response to the environment greater than that of the diploids. Together with the different recombination indices of the polyploids, this may cause short term fluctuating differences to arise between diploids and polyploids.

Polyploids may give rise to new taxa when selective pressures either favour different phenotypes from the ancestral diploids, or when certain selective pressures are reduced or absent. Thus we have the situation in the Annui where certain polyploids (the polycarpic tetraploids) have retained close morphological similarities with the diploids, even though some of them may have quite disjunct distributions; while the other polyploids (the monocarpic tetraploids) have diversified considerably, even though they may be sympatric with the diploids. One main factor may have allowed the

monocarpic tetraploids to evolve in this manner, and that is the inbreeding habit. Removal of the selective maintenance of those characters associated with the outbreeding habit has resulted, in the monocarpic tetraploids, in a reduction in floral part size and number. These changes may be relatively minor in terms of genetic control (this is discussed later in the thesis), but they have made great differences in the appearance of these taxa, and render them easily distinguishable from other members of the Section. Most of the other characters by which the monocarpic tetraploids differ from the majority of the diploids are relatively minor, such as in being phenotypically plastic; in having a tendency towards producing large achenes; and in having a rapid and prolific life cycle. All of these characters can be correlated directly either with polyploidy itself, or with the monocarpic, weedy habit. An exception to this is the glandular habit. Most of the monocarpic tetraploids have a more or less dense epidermal covering of glandular hairs. This character is always reported as absemt from the diploid Eurasian species, although all of those that I have studied (see Materials and Methods), when observed microscopically have proven to possess a low or very low density of glandular hairs. Obvious glandulosity does occur in a few of the diploid Annui, such as S. elegans L. and S. arenarius Thunb., but these South African species are well separated geographically from the Eurasian taxa. Unless an ancestral Eurasian diploid taxon which is now

extinct possessed the glandular habit, the greatly increased glandulosity of some of the monocarpic tetraploids in Eurasia must have arisen by evolution at the tetraploid level. This glandulosity is probably of selective importance, for species with this character appear to be seldom, or never attacked by leaf-miner, or by lepidopteran larvae, and suffer less from aphids than do the non-glandular species. Merz (1959) reported an unidentified chemical in the glandular hairs of S. viscosus which inhibits larvae of Euchelia jacobaea (the cinnabar moth). In the Annui, glandular hairs are abundant only in the Eurasian inbreeding tetraploids, and are sparse, or possibly absent in the Eurasian outbreeding diploids and tetraploids. They are presumably of selective importance, but despite the similarity in geographical and ecological location of many of these species, and hence subjection to similar selective pressures, they only occur in the inbreeders. Glandular hairs are present to some extent in all species which I have studied, and therefore this is not a novel character appearing for the first time in the inbreeders. The difference is one of degree, and the appearance of the character to various degrees of magnitude in the inbreeders may reflect a breeding system which encourages the persistence of gene combinations through subsequent generations. Inbreeding allows the accumulation of individual genes involved in polygenic systems of control of characters, which, if favoured selectively, result in

those genotypes being maintained. Outbreeders, however, are subject to continuous recombination, and although under polygenic control for some characters (e.g. ligule length, - discussed later in the thesis) unless selection is rigid enough to reduce it, recombination will take place at every sexual cycle. The inbreeding habit, especially when associated with the rapid and prolific life cycle of the monocarpic tetraploids, must lead to the predominance of selectively favoured gene combinations to a greater degree than when recombination is partially or fully obligate, as in the polycarpic outbreeding species.

The breeding system is of fundamental importance when speciation is considered. In the Annui the inbreeding species are, in general, easier to separate taxonomically than are the outbreeding species. Although owning a common origin in the inbreeding system the formation of microspecies and species are fundamentally different. In inbreeding taxa with high reproduction rates, the production of wholly or partially sympatric microspecies is continual, and is the normal process in such taxa. All the microspecies share ultimately in a common gene pool. Only when a degree of isolation arises which is sufficient to prevent occasional hybridisation is the formation of potential new species possible. In this sense, therefore, inbreeders do not differ from outbreeders. However, once isolation had occured, inbreeding taxa may be capable of more rapid evolutionary divergence than are outbreeders, due to their

tendencies towards homozygosity and the rapid proliferation of selectively favoured genotypes. Ultimately this will result in reproductive isolation, as suggested by Stebbins (1957) due to the perpetuation and accumulation of genic and chromosomal discontinuities, and the result will be hybrid sterility between the new taxa.

This hypothesis may explain the biosystematic differences between inbreeding and outbreeding taxa in the Annui. The outbreeding taxa are not reproductively isolated (Table 5). By contrast, amoung the inbreeders, P.E. Gibbs (personal communication) has reported embryo inviability in reciprocal crosses between S. vulgaris and S. viscosus. Other hybrids between the inbreeders have not been studied to this extent, but even S. viscosus X S. sylvaticus, the commonest hybrid reported, is virtually sterile (this is discussed later in the thesis). Of the two reported hybrids between tetraploid outbreeders and tetraploid inbreeders, one, at least, was sterile (Table 5).

Relationships between the species groups of the Annui are, however, close; as is indicated by the degree to which hybridity does occur (Tables 5 and 6). In addition to those already discussed, hybrids between diploids and tetraploids occur, and have invariably been reported as being sterile, and when investigated have been shown to be triploid (2n = 30) (see Table 6).

THE GENUS SENECIO IN BRITAIN

About 17 species of Senecio occur in Britain as

Table 6

Reported hybrids between polycarpic diploids and monocarpic tetraploids within Section Annui of Senecio:

Reported hybrid: diploid: tetraploid:	Source:	Comments:
S. vernalis W.& K. X S. vulgaris L. (= S. X pseudovernalis Zabn.)	specimens are in most herbaria with European sections. Most specimens were apparently collected in mid-Europe in the latter half of the 19th. century. See also Vatke (1874); Jacobasch (1894); and Knuth (1908). Reports for the hybrid in Britain (see later text) are thought to apply to the progeny of S. X Baxteri.	in all of these cases the same names have been used to apply to fertile plants resembling ligulate forms of S. vulgaris, as well as the sterile (presumably triploid F_1) hybrid. See discussion in later text.
S. leucanthemifolius Poir. X S. vulgaris L. (= S. X Vaccarii Fiori)	specimens from Sardinia and Italy are in OXF, LIVU, and BM.	
S. squalidus L. X S. vulgaris L. (= S. X Baxteri Druce)	frequently reported in Britain, and specimens are in most herbaria.	
S. squalidus L. X S. viscosus L. (= S. X londinensis Lousley)	frequently occurring in Britain where the two species meet, specimens are in most herbaria.	records, with very few exceptions, refer to the sterile F_1 hybrid.
S. nebrodensis L. X S. viscosus L.	see Acta Hort. Berg. 4(3), 1907; a specimen from Sweden is in BM.	the BM specimen closely resembles S. X londinensis.

natives or established aliens (Appendix Table 6). In addition, about a further 8 species occur fairly frequently as chance introductions (Appendix Table 7), usually as seeds brought in with wool shoddy from Australia or South Africa, or as garden escapes. Other aliens have been recorded on rare or solitary occasions (Appendix Table 8).

A number of other species have been grown horticulturally in this country without being recorded in the wild. These include the hirsute, shrubby senecios (Murphy, 1967, gives an account of these); large, showy, herbaceous bedding plants, such as "Ligularia" (Senecio przevalskii and its relatives); and a few glasshouse plants, the most notable being the florists' "Cineraria" (S. X hybridus, an account of which is given by Barkley, 1966).

Relationships within the genus are fairly clear-cut among the established species in Britain. Substantiated reports only exist of one example of hybrids occurring between species of different Sections of the genus: - S. cineraria X S. jacobaea, respectively of the Sections Cineraria and Jacobaeae (Burbidge and Colgan, 1902). Hybrids are, however, fairly common within particular Sections, as in the Annui (Tables 5 and 6). Unsubstantiated reports of hybrids involving species of the Annui and species from other Sections are given in Table 7. Reports of hybrids exclusive of the Annui in Britain are given in Appendix Table 9. The inability to hybridise with species of other Sections shows that the Annui are a distinct taxon

Table 7 Reported hybrids between British Annui and other Senecio species in Britain:

Reported hybrid:	Source:	Comments:
S. squalidus L. X S. jacobaea L.	specimen in BM from Cork, 1902, stated by F.W. Burbidge as being dwarf, with "bracts nearly entire as in S. Calvescens" (= S. X albescens)	almost certainly a depauperate specimen of S. squalidus
	Praeger (1951): "S. squalidus a south European alien brought along the railway from Cork or Dublin, arrived at Maryborough about 1925 and promptly crossed with S. jacobaea on railway banks there	specimens have not been investigated by me, but lack of other evidence suggests the same interpretation as that above
S. vulgaris L. X S. jacobaea L.	specimen in OXF, collected and identified by Mary Donne, from Aberdovy, 1931. Re-identified by C.G. Druce as S. advena Druce	Donne's identification was based on the plant being infested with cinnabar moth larvae, which are usually specific to S. jacobaea, and that the plant was obviously related to S. vulgaris. It is in fact probably one of the S. vulgaris X S. squalidus segregates refered to later in the text
S. viscosus L. X S. erucifolius L.	specimen in BM from Connington Dump, Wood Walton, Hunts., 1948; also in BSBI Year Book of 1949: 52; and in Watsonia 1(5): 301 - 307 (195)	probably S. viscosus X S. squalidus (= S. X londinensis)
	specimen in BM from Ilford, Essex, 1964	probably a form of S. erucifolius
S. viscosus L. X S. gracilis	specimen in BM, reported by A. Hosking as a spontaneously produced hybrid in the Cambridge Botanic Gardens, 1903	probably S. viscosus

in Britain, with no indications of genetic continuity between themselves and these other species.

Chromosome numbers of native and established Senecio species in Britain are given in Table 8 and Appendix Table 10.

The Section Annui in Britain consists of four native and naturalised species: S. vulgaris, S. sylvaticus and S. viscosus being native or naturalised monocarpic tetraploids (2n = 40); and S. squalidus being a recently established polycarpic diploid (2n = 20). In addition S. cambrensis - the allohexaploid (2n = 60) hybrid from S. squalidus X S. vulgaris arose in North Wales, probably within the last half century, and persists in that locality, apparently having spread very little .

The purpose of investigating the British Annui has been to elucidate the taxonomic relationships of S. squalidus in the British flora. This has fallen into three categories: a comparison of the native Sicilian S. squalidus with the British taxon in order to ascertain whether changes have taken place in the latter taxon; observations of S. cambrensis in order to clarify its status; and studies of other British Annui, in particular S. vulgaris, to see if they have been affected by the advent of S. squalidus.

Table 8 Reported chromosome numbers of British Senecio species of the Section Annui:

Species	n	2n	Reference:	Source of material:
S. squalidus L.	10		Afzelius (1924)	cult. Sweden, ex Sicily
		20	Howard and 'E.A.E.' (1943)	Britain
	10	20	Crisp (unpublished)	Britain and Sicily
S. vulgaris L.	5		Small (1919)	? unsubstantiated counts
	5		Howard and 'E.A.E.' (1943)	Britain
	19		Ishukawa (1924)	Japan
	20		Afzelius (1924)	from 24 separate European populations
		40	Litardiere (1922)	France
		40	Löve and Löve (1956)	Iceland (introduced)
	20		Ornduff et al (1963)	California (introduced)
	20		Ornduff (1964)	Australia (introduced)
		40	Mulligan (1961)	Canada (introduced)
	20		Palmblad (1965)	Washington (introduced)
		40	Gadella and Kliphius (1963)	Netherlands
	20	40	Crisp (unpublished)	counts from about 30 populations, mainly British; including varieties denticulatus and hibernicus
S. viscosus L.	20		Afzelius (1924)	Europe
	20		Palmblad (1965)	France
	20	40	Crisp (unpublished)	counts from about 10 European populations, mainly British
S. sylvaticus L.	20		Afzelius (1924)	Europe
	20		Ornduff et al (1963)	Washington (introduced)
	20		Palmblad (1965)	Washington (introduced)
	20	40	Crisp (unpublished)	counts from 3 British populations
S. cambrensis Rosser		60	Rosser (1955)	North Wales
		60	Harland (1955)	the synthetic allopolyploid
	30	58 59 60	Crisp (unpublished)	North Wales populations, with intra-population, or even intra-plant variation in chromosome number

SENECIO SQUALIDUS

HISTORY OF THE SPECIES

Senecio squalidus was described as a species by Linnaeus (1753). His material was cultivated at Uppsala, in Sweden, and he describes the species as a south European annual, indicating that he was not aware of its precise distribution in southern Italy and Sicily. This lends support to Walker's (1833) statement that Linnaeus obtained seed of the species from the Oxford Professor of Botany, J.J. Dillenius. According to the herbarium record, the species was in cultivation from at least 1690 (Kent, 1956) in the Oxford Botanic Gardens, which opened in 1621 (Darlington, 1963). Smith (1828), however, suggested that there was no proof that Linnaeus' material came from Oxford. A comparison of the British and the Sicilian taxa, as is discussed more fully later, does suggest that Linnaeus' description was drawn up from material very similar to that at present in Britain.

The earliest record that I have found for the species in Britain outside of the Oxford Botanic Gardens is a specimen of "S. muralis, an escape from cultivation, Oxford, 1792" (in CGE, collected by P. Gisborne, ex hb. C.C. Babington). Sibthorp (1794) named plants growing on Oxford walls as a Senecio, and Smith (1799) later identified these as S. squalidus.

Herbarium specimens of S. squalidus for the early 1800's are plentiful, and it was during this period that

the species, as a botanical curio, was introduced into several new localities in the British Isles. Its subsequent spread was rapid, until at the present time it is common in England, Wales, and Ireland, and has begun to appear in Scotland and several north west European countries. A vice county list, recording the spread of the species until 1930 is given in Appendix Table 11.

The rapid spread of S. squalidus following at least a century of quiescent cultivation in the Oxford Botanic Gardens has invited comment from several quarters. No definite suggestions have been made as to the reason for this sudden success, although much of the species' subsequent spread has been attributed to seed dispersal along the growing railway system.

The records of the Oxford Botanic Gardens in the 1700's have unfortunately been lost (K. Burras, personal communication), and this together with a lack of herbarium data means that no direct evidence exists concerning any related taxa which might have been grown with S. squalidus; or, indeed, to exclude the possibility that S. squalidus was introduced more than once. It therefore was desirable that a comparison should be made between the Sicilian and the British taxa.

THE SICILIAN SENECIO SQUALIDUS

Investigations of herbarium material (BM, K, OXF, MANCH) of the Sicilian Senecio squalidus were only of partial help in trying to assess the morphological range of the species, and so live material was used from three sources:

1. One seed sample from L.E. Newton, collected at Catania, Sicily, in 1964.
2. 32 seed samples donated by Professor E. Poli and Dr. H. Ronsisvalle of Catania University, believed to have been collected in 1967.
3. My own collections from the Mt. Etna region of Sicily, in June, 1968.

Seed samples from the first two sources were not specifically recorded as to their locality of collection. My own samples were collected from the localities given in Table 9 and Figure 1.

Field observations were also made in Sicily, and will be discussed later. In addition, herbarium specimens were collected, and, together with specimens grown from seed samples, are in my personal herbarium. Photographs were taken, and live plants were collected, but most of the latter died in transit back to Britain.

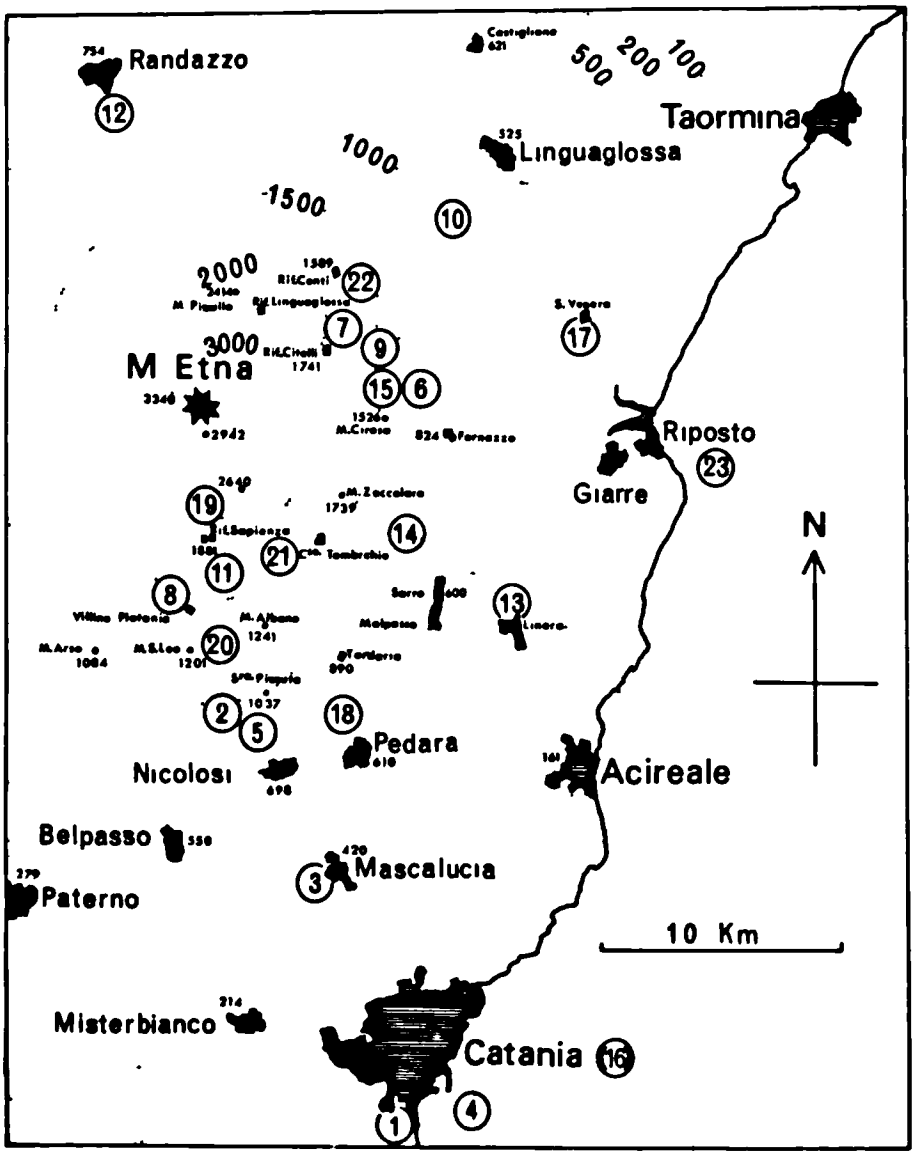
The species in Sicily falls into three categories, of debatable taxonomic status. These are: the montane taxon, restricted to the upper 2,500 m. (above about 1,000 m. above sea level) of Mt. Etna; the lowland taxon,

Table 9 Locations of Sicilian collections of Senecio aetnensis/S. chrysanthemifolius:

locality: numbers refer to Fig. 2	habitat	altitude (in metres)
1 Syracuse road, 1 Km. S. of Catania	waste ground, open vegetation	ca. 50
2 Etna road, 3 Km. N.W. of Nicolosi	roadside, open vegetation	ca. 850
3 Mascalucia, near Catania	recently cultivated ground	420
4 Catania Docks	waste ground, open vegetation	ca. 20
5 Etna road, 2 Km. N.W. of Nicolosi	roadside vegetation	ca. 800
6 Etna road, 2 Km. N.W. of Fornazzo	open vegatation on laval soil	ca. 900
7 by Rif. Citelli, Mt. Etna	sparse vegetation on laval slopes	ca. 1750
8 near Villino Platania, Etna road from Nicolosi	open vegetation on laval soil	ca. 1400
9 2 Km. E. of Rif. Citelli, Mt. Etna	in open birch scrub on laval soil	ca. 1500
10 4 Km. S.W. of Linguaglossa, Mt. Etna	open vegetation on laval soil	ca. 1000
11 near Rif. Sapienza, Mt. Etna	sparse vegetation on laval slopes	ca. 1800
12 1 Km. S. of Randazzo	open roadside vegetation	ca. 850
13 near Linera	roadside vegetation	ca. 200
14 Etna road, 3 Km. N.W. of Sarro	cultivated ground by vineyard	ca. 900
15 4 Km. W.N.W. of Fornazzo, Mt. Etna	open laval soil	ca. 1100
(16) Catania	weathered, dry laval soil	probably 200
17 near S. Venera	roadside vegetation	ca. 200
18 near Pedara	waste ground	ca. 600
19 near Rif. Sapienza, Mt. Etna	sparse vegetation on laval slopes	ca. 2300
20 2 Km. S.E. of Villino Platania, Mt. Etna	open vegetation on laval soil	ca. 1000
21 2 Km. W. of Cse. Tomarchio, Mt. Etna, and neighbouring area	pioneers on disused roadway, laval substrate	ca. 1500 - ca. 1800
22 near Rif. Conti, Mt. Etna	open vegetation on laval soil	ca. 1600
23 Riposto	waste ground	ca. 50
(24) Canalucehio	?	700
(25) Sona	?	1500

Figure 1

Mt. Etna and neighbouring districts altitudes are given in metres above sea level; ringed numbers refer to sites of collection of Senecio aetnensis/ S. chrysanthemifolius



common in Sicily and south Italy; and an intermediate taxon occuring in the foothills and lower slopes of Etna (about 500 - 1,500 m. above sea level). The Italian botanists apparently treat these three taxa as separate species (Pojero, 1902; E. Poli and H. Ronsisvalle, personal communication): with S. chrysanthemifolius Poir. as the lowland species; S. incisus Presl. (= S. glaber Ucria) as the intermediate, typically occuring in the wooded region of Etna; and S. aetnensis Jan. as the montane species. S. aetnensis and S. incisus are endemic to Mt. Etna (Poli, 1959).

Poli suggested (personal communication) that these species bore fruit at different times of the year, ranging from May to August. Observations of herbarium material in this country, however, showed a considerable overlap in flowering and fruiting times, and when I visited Sicily in mid-June, 1968, all three taxa were (fortunately) in seed, and appeared to be of about the same ontogenetic age.

S. incisus appeared, from my observations, to occur at about 1,000 ± 200 m. above sea level, and always marked the upper limits of local S. chrysanthemifolius, and the lower limits of local S. aetnensis. One of Dr. Ronsisvalle's seed specimens, however, was labelled as "S. incisus, Sona, 1,500 m."; and some herbarium specimens are of plants resembling S. incisus (at least in leaf shape, - see later text) from as low as Catania itself (MANCH, K, and CAT), and as high as 6,000 - 8,500 feet

(= 1,850 - 2,600 m. above sea level) on Mt. Etna (MANCH, K, BM, and CAT). My own observations (see Figure 1) were restricted to the eastern half of Mt. Etna, and do not necessarily infer that the situation is the same elsewhere. Additionally, of course, the wind dispersed papillate achenes of the plants might give rise to colonies outside of the usual altitude range of a particular taxon, if other conditions permitted it.

My impressions in Sicily were that S. incisus was, in fact, a series of hybrid swarms between S. aetnensis and S. chrysanthemifolius, and that probably a degree of gene flow takes place between the latter two species. Listed in Table 10 are my field observations of the differences between what were taken to be the most extreme forms of S. aetnensis and S. chrysanthemifolius that I saw. Plate 1 shows capitula of two of these extreme forms, grown from seed collected on Mt. Etna. S. incisus, as already stated, occurred in localities between these two species, and formed a series of intermediates with respect of glaucosity, leaf dissection, and ligule size. These three characters were the most obvious differences between S. aetnensis and S. chrysanthemifolius, and usually formed a basis for field identification. A good correlation is shown by these characters in relation to altitude by Figures 2 and 3, the data being drawn from the cultivated progeny of seed collected in Sicily. The leaf dissection types referred to in Figure 2 are given in Figure 4.

Similar correlations with altitude can be made with

Table 10

Field observations (in Sicily) of the differences between *Senecio aetnensis* and *S. chrysanthemifolius*:

Character:	*S. aetnensis*:	*S. chrysanthemifolius*:
habitat	montane (Mt. Etna); larval slopes at > 1,000 m. a.s.l.	lowland; disturbed habitats at < 1,000 m. a.s.l.
aerial parts	glaucous	non-glaucous
	glabrous	slightly pilose
leaf shape	spathulate, oblong or elliptical	more or less rhomboid in outline
dissection	serrate to dentate	deeply pinnatifid to bi-pinnatifid; lobes narrow, entire or irregularly serrate or dentate
auricles	entire to serrate, large and amplexicaul	deeply dissected, small or occasionally absent
capitulum size	large (ca. 9 mm.long x ca. 7 mm. broad)	small (ca. 7 mm. long x ca. 5 mm. broad)
inner involucral bract tips	usually colourless; an occasional purple colouration when immature subsequen-tly disappears	black
ligule size	large (ca.12 mm.long x ca. 4 mm. broad)	small (ca. 8 mm.long x ca. 3 mm. broad)
achene size	long (ca. 4 mm.)	short (ca. 2.5 mm.)
surface	glabrous	hairy in grooves
colour	light brown	dark brown
persistence	* persistent	* non-persistent
pappus length	long (ca. 9 mm.)	short (ca. 5 mm.)
seed set	* high (often 80%)	* low (often 10%)
growth habit	* much branched, but often semi-prostrate	much branched, and ascending

Note: An asterisk (*) denotes that these characters were apparently environmentally controlled, for they were not observable under constant (glasshouse) conditions: the persistence of the achenes may have been a response to climatic conditions (e.g humidity); the growth habit to climatic or edaphic factors; and seed set was probably a response to the availability of pollinating insects - both species are self-incompatible and insect pollinated, but *S. aetnensis* is a conspicuous plant of open habitats, and *S. chrysanthemifolius* is inconspicuous and inhabits more closed habitats, placing it in unfavourable competition with many other insect-attracting species.

Plate 1 Capitula of *Senecio aetnensis* and *S. chrysanthemifolius*:

A

B

Both plates are X 3.3; divisions in the background are cm..
A is *S. aetnensis* (specimen E70:1): note the large capitula and ligules, and the glaucosity;
B is *S. chrysanthemifolius* (specimen E96:5): note the black tips on both inner and outer involucral bracts.
On floral characteristics, the scoring (cf. Table 13) of E70:1 and E96:5 was as follows (*S. aetnensis* scores 0; *S. chrysanthemifolius* 10):

	ligule		capitulum		bract		
	length	breadth	length	breadth	tips	glaucosity	TOTAL
E70:1	0	1	2	3	0	0	6
E96:5	7	7	5	8	10	10	47

FIGURE 2

Leaf dissection and glaucosity of progeny from the *Senecio aetnensis* / *S. chrysanthemifolius* complex in Sicily, related to altitude up Mt. Etna of the parental material: (○ = non-glaucous; ◍ = slightly glaucous; ● = glaucous)

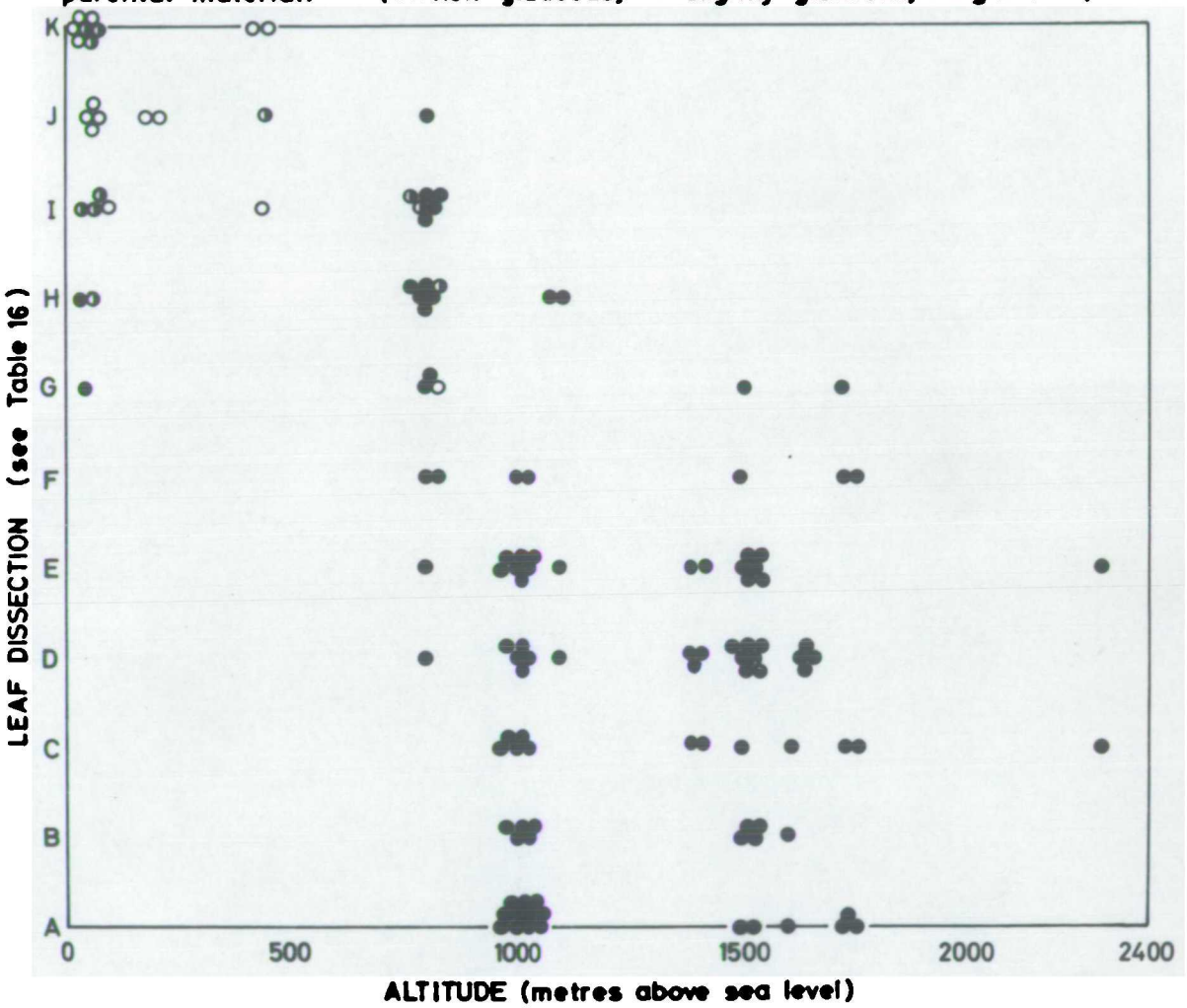


FIGURE 3

Ligule dimensions of progeny from the Senecio aetnensis / S. chrysanthemifolius complex in Sicily, related to altitude up Mt. Etna of the parental material:

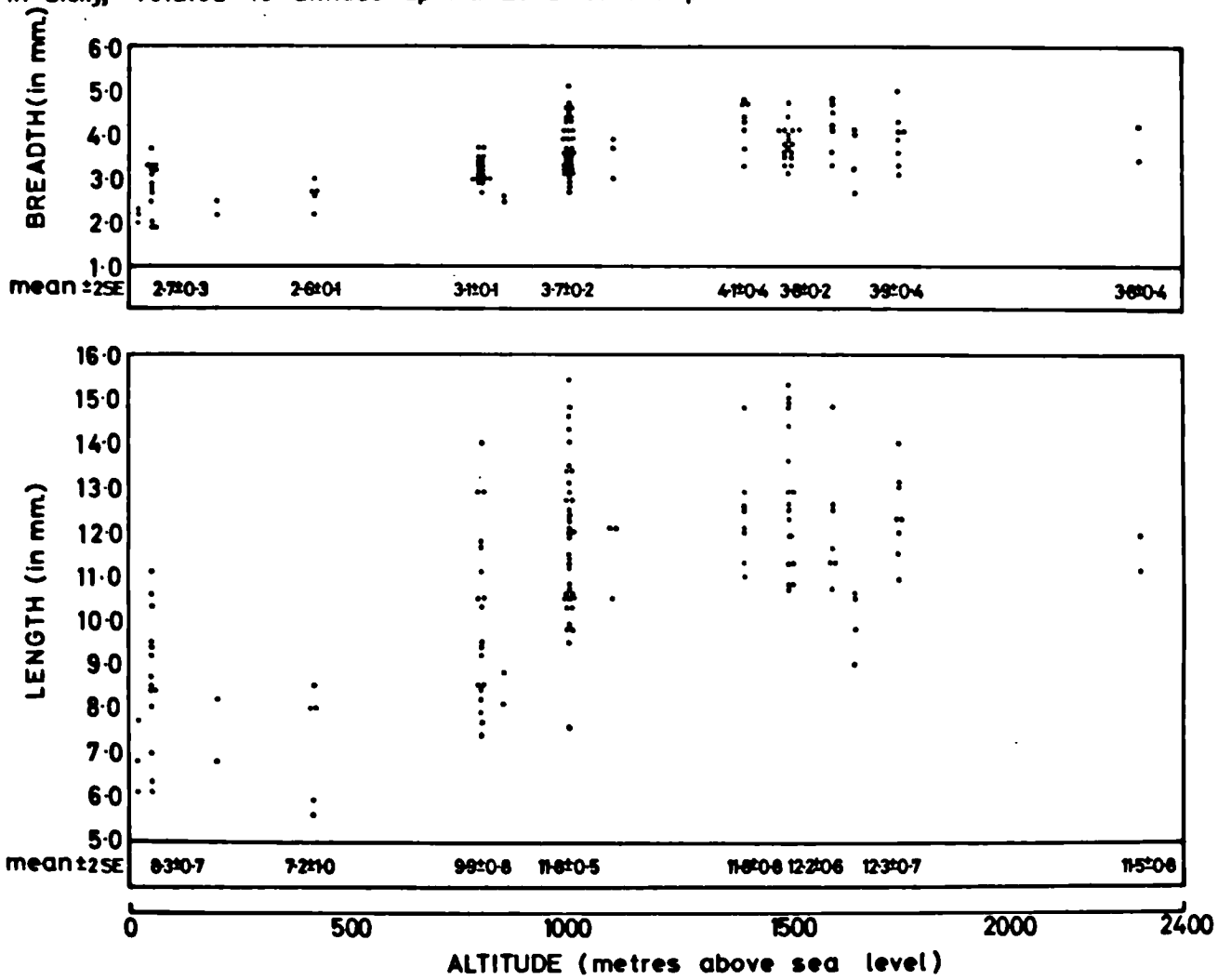
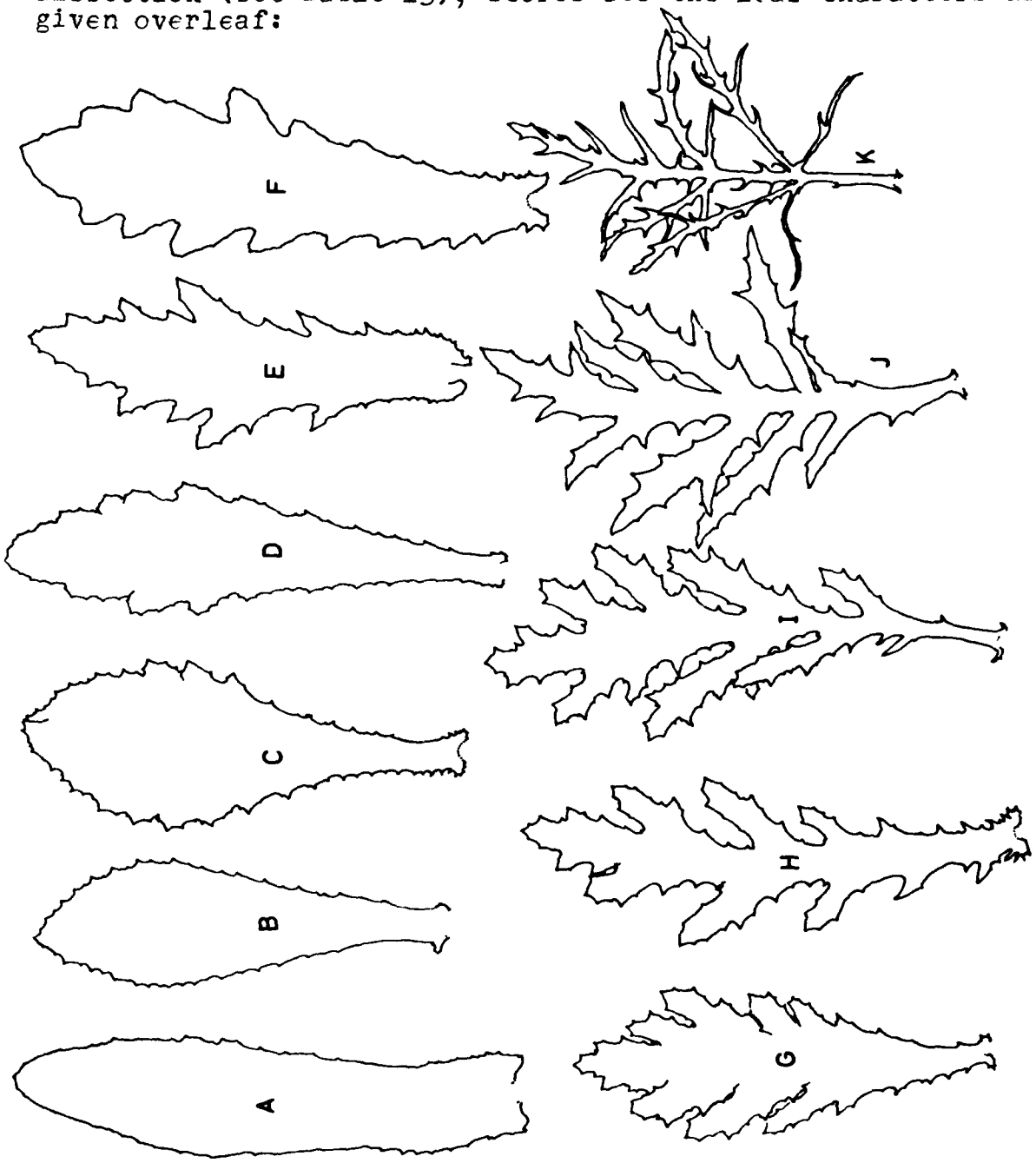


Figure 4 A selection of the middle cauline leaves of Senecio aetnensis and S. chrysanthemifolius and their intermediates: - the letters A - K refer to their degree of dissection (see Table 13); scores for the leaf characters are given overleaf:



- see overleaf -

Notes on Figure 4 :

1. The following leaves are from progeny of the same plants:
   B, C, and E from E94 (identified in the field as S. aetnensis);
   G, and H from E37 (identified in the field as S. "incisus").
   - this is an indication of the extent of recombination taking place under conditions of natural pollination on Mt. Etna.
2. Leaf dissection type F was found in plants in several localities. The extent of dissection is very close to that of type E, but the teeth are non-prominent, thus giving the leaf lobes a rounded appearance and slightly decreasing the apparent degree of dissection of the leaf.
3. Scores (cf. Table 13) for leaf characters: - S. aetnensis scores 0, and S. chrysanthemifolius scores 10:

	Leaf no.:										
	A	B	C	D	E	F	G	H	I	J	K
Character:	Score:										
dissection	0	1	2	3	4	5	6	7	8	9	10
outline shape	0	0	3	0	0	0	3	0	6	10	10
auricle size	0	5	5	5	2½	2½	5	2½	5	5	7½
TOTAL:	0	6	10	8	6½	7½	14	9½	19	24	27½

---

most of the characters in Table 10. Thus, in the cultivated progeny of the Etnan plants, capitulum size, involucral bract tip colour, and achene length, colour, and hairiness could all be correlated with altitude (Figures 5, 6, and 7). Glaucosity and hairiness appeared in Sicily to be mutually exclusive, and this was established in the cultivated plants, although a few intermediate plants were observed with reduced glaucosity and hairiness, often together.

A number of characters separating S. aetnensis and

FIGURE 5

Achene length, colour, and glabrosity of progeny from the Senecio aetnensis / S. chrysanthemifolius complex in Sicily, related to altitude up Mt. Etna of the parental material: (△ = hairy in grooves; ○ = glabrous; △, ○ = light brown; ▲, ◑ = mid brown; ▲, ● = dark brown)

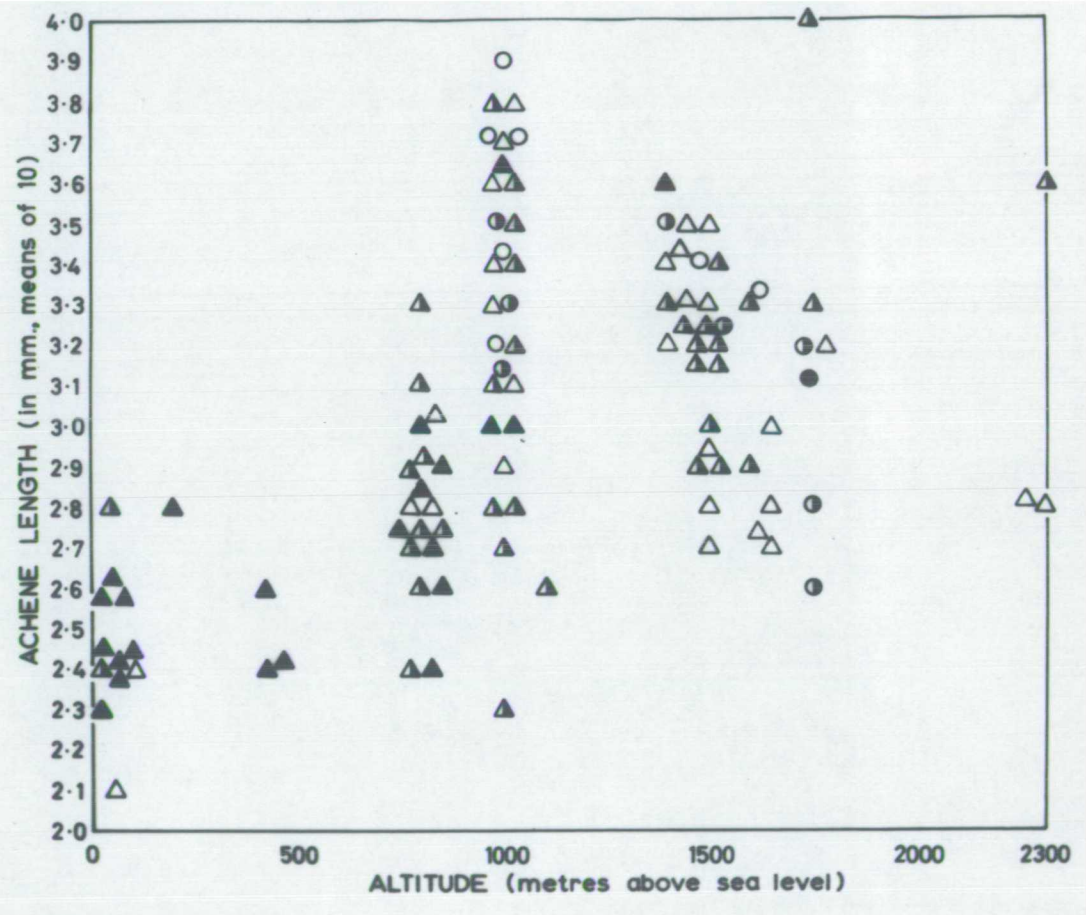


FIGURE 6

Blackness of inner involucral bract tips of progeny from the Senecio aetnensis / S. chrysanthemifolius complex in Sicily, related to altitude up Mt. Etna of the parental material:

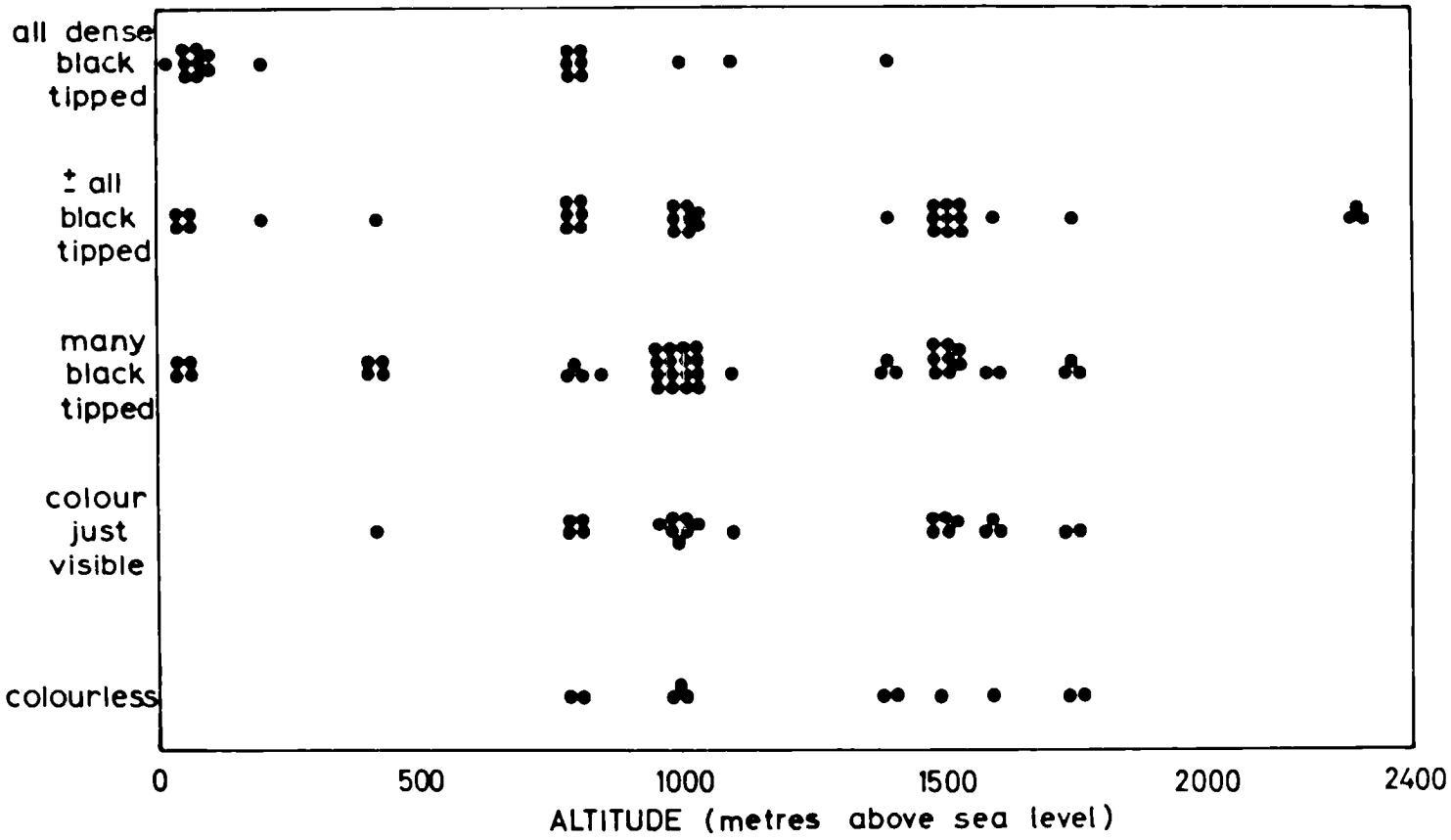
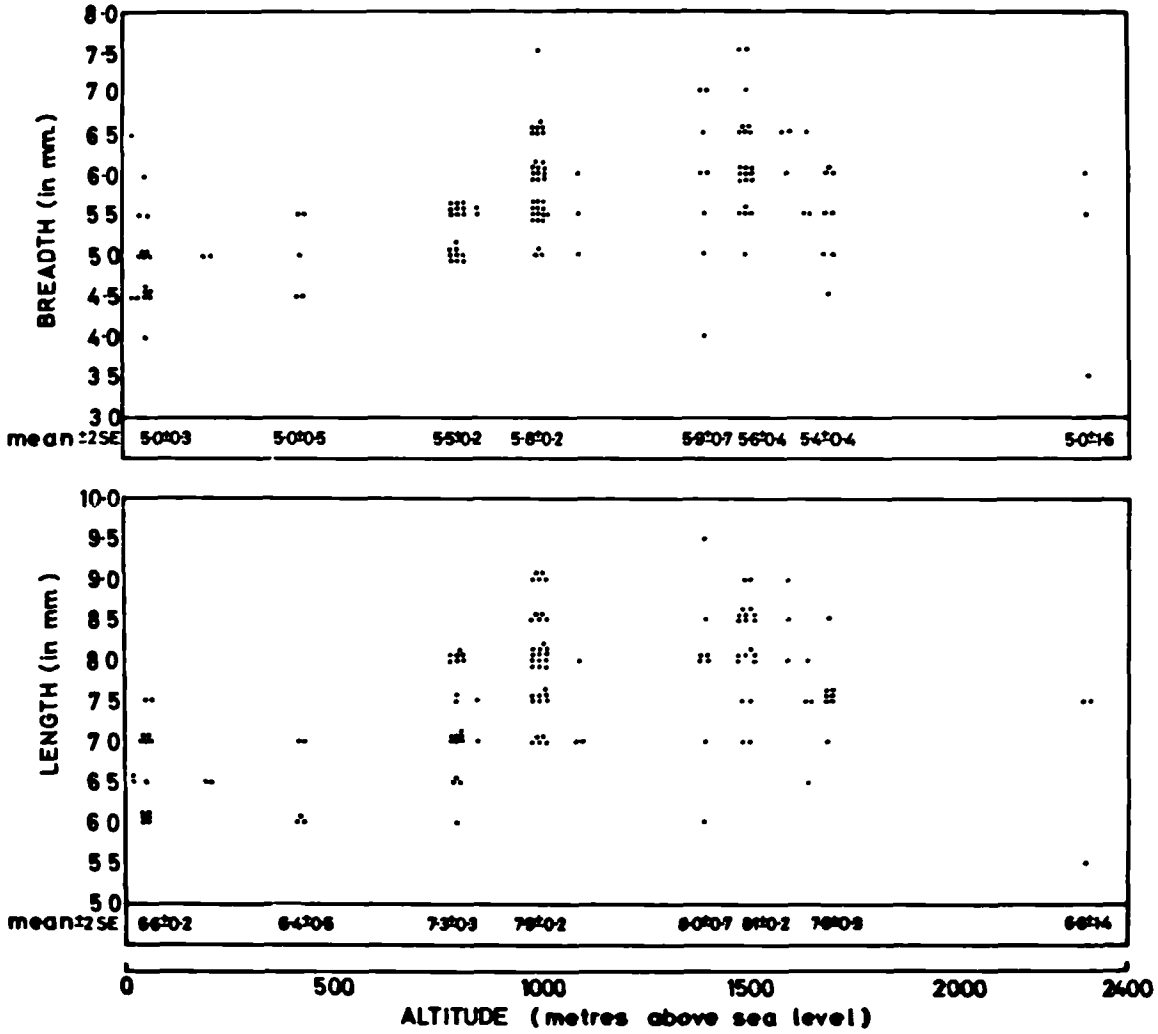


FIGURE 7

Capitulum dimensions of progeny from the Senecio aetnensis / S. chrysanthemifolius complex in Sicily, related to altitude up Mt. Etna of the parental material:



S. chrysanthemifolius in the field were apparently under environmental control. The fleshy leaves and creeping habit often seen in the montane S. aetnensis were not apparent when grown in the glasshouse, these presumably being growth forms associated with exposure at high altitudes. The persistence of ripe achenes on the receptacle shown by S. aetnensis might also have been a response to climatic factors.

The difference in seed set between the two taxa was probably a response to the availability of pollinating insects. My observations on progenies grown in Britain show both taxa to be self-incompatible and must be insect pollinated in the field. S. aetnensis is a conspicuous plant of open habitats, and S. chrysanthemifolius is inconspicuous and inhabits more closed communities, placing it in relatively unfavourable conditions with many other insect-attracting species.

Correlations of several characters with altitude are given in Table 11.

It appears, from the distribution of the various characters with altitude, that a bipolar gene flow is taking place, presumably via both seed and pollen dispersal. The character differences between S. aetnensis and S. chrysanthemifolius observable on Etna can be divided into several categories: some are only fully expressed as a response to environmental factors; others are not effected in their expression to a great degree by the environment, and are subject to varying degrees of selection

Table 11 Analyses of variance of the progeny of *Senecio aetnensis*/*S. chrysanthemifolius*

	Df	Ss	Ms	Vr	significance
1. ligule number versus morphological score:					
between degrees of score	11	49.30	4.48	2.19	significant at the 5% level
within degrees of score	92	188.66	2.05		
total	103	237.96	2.31		
2. ligule number versus altitude of parent:					
between degrees of altitude	9	23.74	2.64	1.20	not significant at the 20% level
within degrees of altitude	123	270.63	2.20		
total	132	294.37	2.23		
3. ligule breadth versus altitude of parent:					
between degrees of altitude	9	30.04	3.34	13.09	significant at the 1% level
within degrees of altitude	121	30.83	0.26		
total	130	60.87	0.47		
4. ligule length versus altitude of parent:					
between degrees of altitude	9	222.95	24.77	9.21	significant at the 1% level
within degrees of altitude	120	323.07	2.69		
total	129	546.02	4.23		
5. bract tips (scored 1 - 5) versus altitude of parent:					
between degrees of altitude	9	194.27	21.59	7.32	significant at the 1% level
within degrees of altitude	123	362.38	2.95		
total	132	556.65	4.22		

(Table 12). The selectively controlled, and environmentally affected factors must enhance the phenotypic differences between the lowland and montane taxa in the field, and to some extent support the taxonomic separation of S. aetnensis and S. chrysanthemifolius. Analysis of these characters has been made on the progeny of the plants from the field, and thus the genetic constitution of the field plants has been measured. The continuity of genetically controlled characters has been established, even though these characters may appear to be disjunct in the field. Those characters which are genetically disjunct (hairiness of achenes; leaf dissection) must be those subject to rigid selection, as other characters (achene colour; size of ligules) show a clinal distribution through the entire population studied, and indicate that gene flow does take place to a considerable extent.

The characters separating S. aetnensis and S. chrysanthemifolius were scored using the scheme detailed in Table 13, The results are expressed against altitude in Table 14and Figure 8(a). They show the degree to which intergradation of character differences between the two taxa has taken place, within the limitations of a scoring system involving no weighting of characters. Figure 8(a) indicates that reciprocal gene flow is taking place between S. aetnensis and S. chrysanthemifolius, and that the region of highest hybridity is at about 800 m. above sea level, - which corresponds to the field observations in Sicily.

Table 12

Environmentally and genetically cotrolled differences between Senecio aetnensis and S. chrysanthemifolius in the field (cf. Table 10):

Character:	Control:	Reasons:
semi-creeping habit often seen in S. aetnensis	completely dependent on environmental conditions for expression	not seen when under cultivation in glasshouse
persistent achenes of S. aetnensis		
fleshy leaves of S. aetnensis		
achene colour	under weak selective pressure; expression not affected by environment	possess a clinal distribution when subject to genetic analysis (see Figs. 6 & 5); and no clear disjunction in the field
achene size		
bract tip colouration		
large ligules of S. aetnensis	under weak selective pressure; and some environmental control	fairly clear disjunction in the field, but genetic analysis reveals a more clinal nature (see Fig. 3)
hairy achenes of S. chrysanthemi-folius	strongly selected for in lowland habitat	glabrous achenes not seen in field lowland plants or their progeny (see Fig. 5)
reduction of leaf dissection in S. aetnensis	strongly selected for in the montane habitat	montane plants in the field, or their progeny are nearly always glaucous, and with more or less entire leaves (see Fig. 2)
glaucosity of S. aetnensis		
possible 8¾ligule state in S. aetnensis vs. 13-ligule state in S. chrysanthemi-folius	selectively favoured in all habitats; ancestral character in S. aetnensis	occurs rarely in S. aetnensis (Figs. 8(c), and 9)

TABLE 13

Scoring of characters of Senecio aetnensis and S chrysanthemifolius

	S. aetnensis SCORE S chrysanthemifolius																					
	0	2/3	1	1 1/3	2	2 1/2	2 2/3	3	3 1/3	4	4 2/3	5	5 1/3	6	6 2/3	7	7 1/3	7 1/2	8	8 2/3	9	9 1/3	10
character																							
leaf dissection, see Figure	A		B		C			D		E		F		G		H			I		J		K
leaf shape in outline see Figure	long-spathulate to oblong								spathulate to narrow elliptical						elliptical								rhomboid
hairiness of leaves and stems	glabrous											hairs just discernable											slightly hairy
glaucosity of leaves and stems	glaucous											slightly glaucous											non-glauc-ous
relative leaf auricle size, see Figure	very large					large						medium size						small					absent
mean achene length (in mm)	>3.9	3.9		3.8	3.7		3.6		3.5	3.4	3.3		3.2	3.1	3.0		2.9		2.8	2.7		2.6	<2.6
hairiness of achenes	glabrous								sparse, in grooves						medium, in grooves								dense, in grooves
achene colour	light brown											mid brown											dark brown beneath hair
inner involucral bract tips	colourless					colour just visible						many black tipped						± all black tipped					dense black tips
inner involucral bract length (in mm)	10.0		9.5		9.0			8.5		8.0		7.5		7.0		6.5			6.0		5.5		5.0
receptacle breadth (in mm.)	8.5		8.0		7.5			7.0		6.5		6.0		5.5		5.0			4.5		4.0		3.5
ligule length (in mm.)	<15.5		<14.5		<13.5			<12.5		<11.5		<10.5		<9.5		<8.5			<7.5		<6.5		<5.5
ligule breadth (in mm)	<5.2		<4.9		<4.6			<4.3		<4.0		<3.7		<3.4		<3.1			<2.8		<2.5		<2.2

Table 14

Field collections (in Sicily) of *Senecio*, together with the scores (see Table 13) of their progeny:

locality no. (see Figure 1)	specimen code no.	field identification	altitude above sea level (in metres)	score of progeny to nearest whole number, with *S. aetnensis* = 0, and *S. chrysanthemifolius* = 130
4	E45	*chrysanthemifolius*	ca. 20	106 103
23	E96	*chrysanthemifolius*	ca. 50	77 90
1	E20	*chrysanthemifolius*	ca. 50	120
	E38			67 74
	E40			105 101 94 82
	E41			103
13	E1 - E4	*chrysanthemifolius*	ca. 200	
17	E83	*chrysanthemifolius*	ca. 200	
(16)	E150	(squalidus)	prob. 200	108
3	E42	*chrysanthemifolius*	420	
	E43			108 108 112
	E44			
18	E57	*chrysanthemifolius /incisus*	ca. 600	
	E21 - E36	*chrysanthemifolius*	700	
5	E98	*chrysanthemifolius*	ca. 800	86 82 82 90
	E101	*chrysanthemifolius*		
	E100	*chrysanthemifolius /incisus*		75 73 76
	E97	*chrysanthemifolius /incisus*		57
	E56	*incisus*		56 54

- continued -

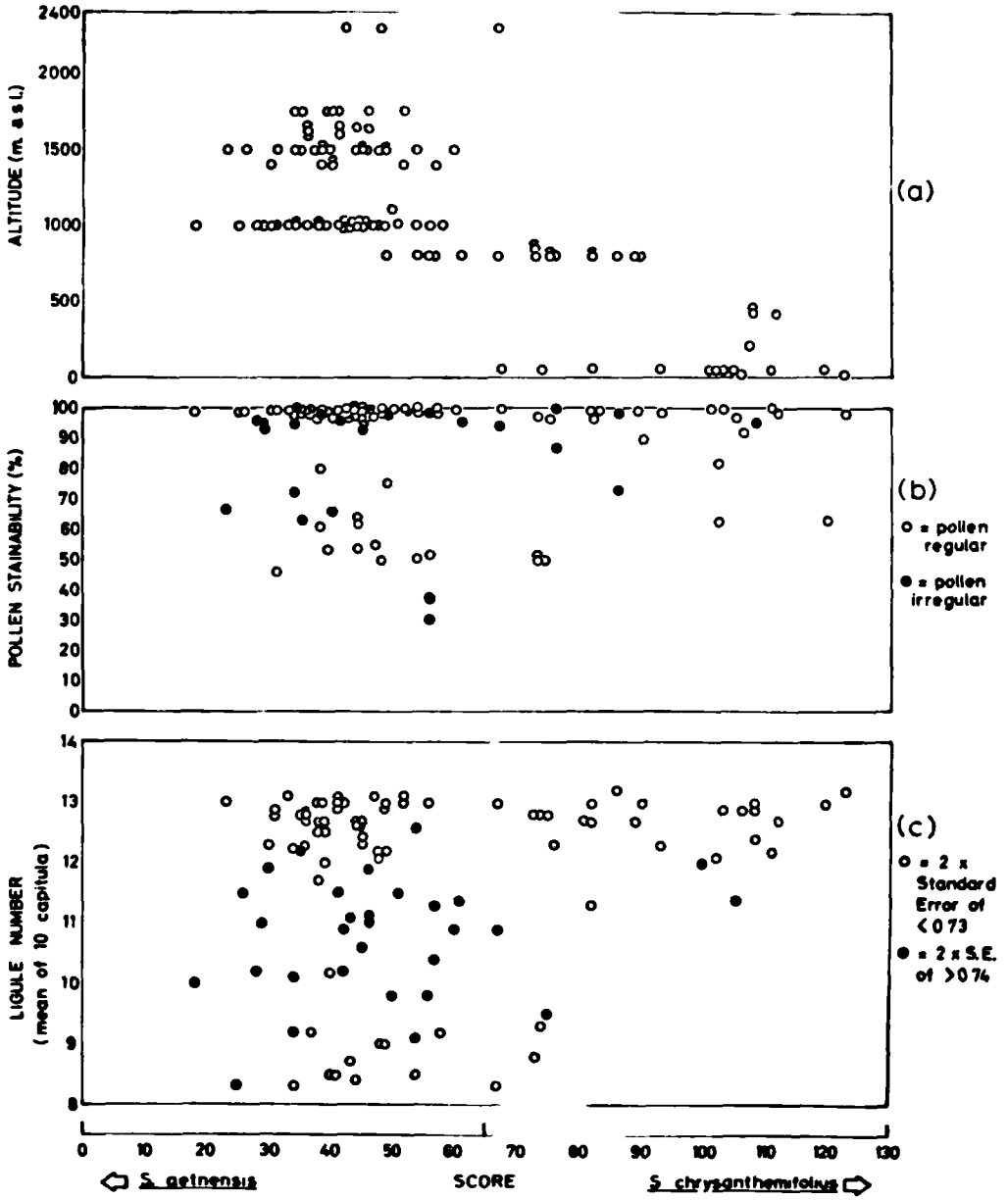
5	E99	incisus	ca. 800	61 67 75 89 49
12	E131	incisus	ca. 850	
2	E37	incisus	ca. 850	73 73
14	E39	incisus	ca. 900	
6	E60	aetnensis	ca. 900	
10	E82	aetnensis	ca. 1000	28 25 34 18
	E85			
	E87			
	E88			31 48 39 47
	E89			43 44 43
	E90			36
	E91			42 41 38 54
	E92			30
	E94			51 42 49 44
	E95			34 29 38
20	E61	aetnensis	ca. 1000	56 58 45 45 33
15	E55	incisus	ca. 1100	
	E59			
	E58			
	E84	aetnensis /incisus		50
8	E65	aetnensis	ca. 1400	40 40 57
	E73			
	E70			38 30 52
(25)	E5 - E17	(incisus)	1500	
9	E93	aetnensis /incisus	ca. 1500	49 48 45 37 48
	E74	aetnensis		39 35
	E75			23 38 34
	E76			38
	E77			43 54 46 45
	E78			

- continued -

9	E79	aetnensis	ca. 1500	
	E80			
	E81			26
22	E86	aetnensis	ca. 1600	36 41 36
21	E72	aetnensis (seed from many plants)	ca. 1500 - ca. 1800	41 36 46 44
	E71	aetnensis ?/incisus?	ca. 1700	
7	E62	aetnensis	ca. 1750	34 35 39
	E64			46 41 52 39
	E46 - E54	(aetnensis)		
11	E130	aetnensis	ca. 1800	
19	E18	aetnensis	ca. 2300	48 42 67
	E19			
	E63			

FIGURE 8

Scores (cf Table 18) of progeny from the Senecio aetnensis / S chrysanthemifolius complex in Sicily, related to altitude up Mt Etna of the parental material (Figure 8 a), pollen stainability (Figure 8 b), and numbers of ligules per capitulum (Figure 8 c)



It would be of interest to compare south Italian populations of S. chrysanthemifolius with those of Sicily in order to assess the extent of this introgression.

HYBRIDISATION BETWEEN S. AETNENSIS AND S. CHRYSANTHEMIFOLIUS

In an effort to assess the effect of hybridisation between S. aetnensis and S. chrysanthemifolius, two series of observations were carried out: one on the morphologically intermediate plants grown in the glasshouse from seed collected in Sicily; and one on the hybrids produced by crossing S. aetnensis and S. chrysanthemifolius under experimental conditions.

1. THE NATURAL S. INCISUS

Morphologically intermediate plants corresponding to S. incisus were investigated for indications of the effects of hybridity. These included meiotic disturbances, pollen sterility, and morphological abnormalities, in particular the occurence of reduced or variable numbers of ligules per capitulum. The intra-individual morphological variability of Senecio hybrids is discussed later in the Chapter dealing with S. viscosus X S. squalidus (p. 197). It is sufficient to mention here that I had noticed that various Senecio hybrid progeny showed variable (usually reducing from normal) numbers of ligules per capitulum when compared with parental individuals. Observations in Sicily that ligule number varied from (7 -) 8 - 13 (- 15) im individual plants (the usual number is 13) prompted the use of this criterion

as a possible measure of hybridity.

Investigation of pollen mother cell meiosis revealed no irregularities, and for the approximately 30 plants studied, the chromosome number was determined as n = 10 on every occasion (this data is included in Table 27, pp.138-9).

It was noted that two main types of pollen infertility occurred: in one (Plate 2(a)), the grains, whether stained or not were of uniform size, and most samples were of 50±3% stainability; in the other (Plate 2(b)), unstained grains ranged from less than 1% to more than 98% of the total, and varied considerably in size, as did the stained grains. In the latter case pore numbers could vary from one to at least 8, as opposed to the usual number of three. The reasons for these quite distinct types of pollen were not apparent in meiotic abnormalities, and are therefore presumably genic or cytoplasmic in nature. The type with uniform 50% unstained grains suggests a simple Mendelian, lethal segregant. This situation is probably analogous to that reported in wheat by Sears and Loegering (1961) of a mutant gene termed "pollen killer" which operates gametophytically in heterozygous individuals, killing 50% of the pollen. The irregular type of pollen sterility may be due to a sporophytic factor, which may be effected by environmental conditions, and which results in varying degrees of pollen formation. This is supported by occasional inconsistencies in the frequency of unstained grains of plants with irregular pollen: one plant in

Plates 2a and 2b

Different types of pollen sterility in progeny of the Sicilian Senecio aetnensis/S. chrysanthemifolius complex:

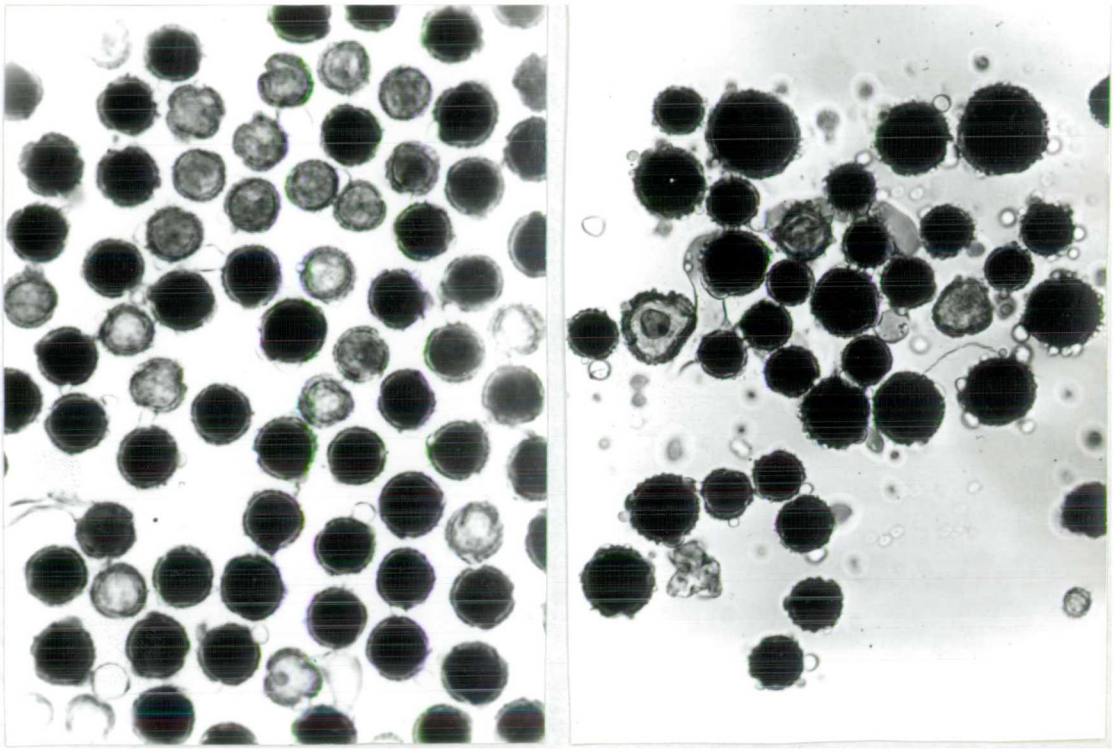


Plate 2a Plate 2b

Plate 2a shows regular pollen of the type which often occurs with 50% of the pollen unstained. The specimen is from plant E38:4, which had 49.7% pollen stained, with the stained grains measuring 27.1μ with 2 X Standard Error of 0.4μ and range of 25.1μ - 30.7μ.

Plate 2b shows irregular pollen. The specimen is from plant E95:1, which had 86.3% pollen stained, with the stained grains measuring 30.1 ±1.7μ, range 23.3μ - 53.0μ.

In both cases preparations were made in cotton blue/ lacto phenol, and magnification of the photographs is X 300.

particular gave 98.1%, 36.4%, and 29.9% unstained grains in counts of about 1,000 from three different capitula.

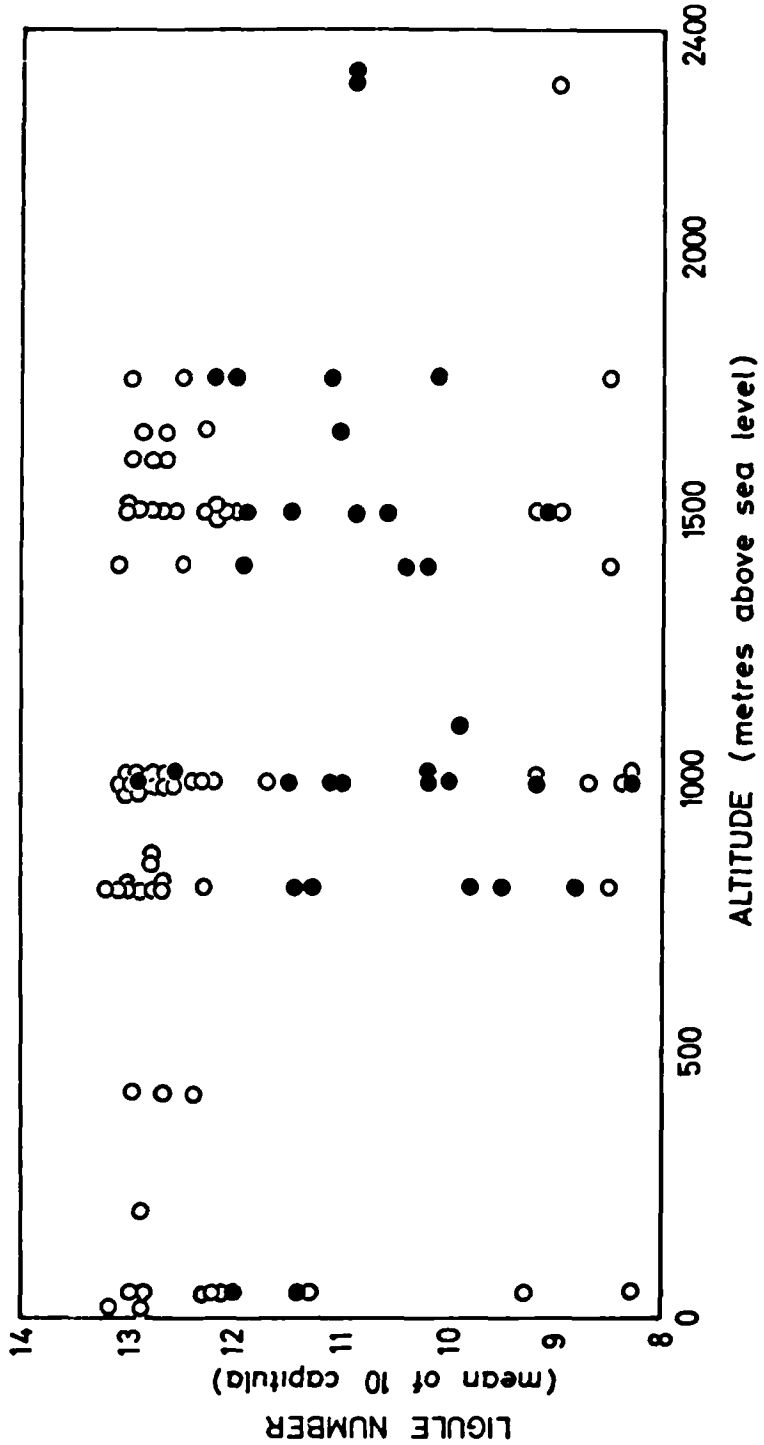
Both types of pollen sterility were widespread. In neither case was a correlation noted with seed sterility, indicating that both phenomena were probably restricted in their effects to the pollen. Complete, or partial male sterility may be an adaptive measure to increase recombination in hermaphrodite plant populations. The self-incompatibility system of the Etnan taxa, however, must ensure maximum recombination at each generation. The reasons for the widespread occurrence of the two types of pollen sterility are not apparent.

Reference to Figure 8 shows that no correlation could be made between pollen sterility, or pollen type and the degree of hybridity of the plants (Figure 8(b)); or between the mean number of ligules per capitulum, or their intra-plant variability, and the degree of hybridity (Figure 8(c)).

Three interesting observations can, however, be made from Figure 8. The absence of a correlation of pollen unstainability with hybridity indicates the probable close chromosomal homology between the taxa involved, and the widespread distribution of the two types of pollen abnormality is another indication of genetic continuity throughout the whole population. The distribution of mean ligule numbers in Figure 8(c) raises the possibility that the 8-ligule character is one of the ancestral characters of S. aetnensis, which is being selectively replaced by the 13-ligule character from S. chrysanthemifolius. This is

FIGURE 9

Ligule number and variability per capitulum of progeny from the Senecio aetnensis / S. chrysanthemifolius complex in Sicily, related to altitude up Mt. Etna of the parental material (O = 2 x Standard Error of <0·73; ● = 2 x S E of >0·74):



suggested by the rarity of mean ligule numbers of less than 12 in plants with scores of more than 80 (that is, those at the S. chrysanthemifolius end of the scale); and the high frequency of mean ligule numbers of 8 and 9 in plants with scores of less than 80. The 13-ligule character may offer selective advantages in attracting insects. The character is, in fact, not correlated with altitude as much as with the genetic constituency of the plants (compare Figure 9 with Figure 8(c) and see Table 11, p 51), and appears therefore to be selectively favoured in those populations where the flowers are less likely to be visited by insects: - that is in the more closed communities.

The predominance of plants with large variability in ligule numbers (as is indicated by high standard errors) in the mean ligule range of 9 to 12 may support the use of the criterion as a measure of hybridity, although it has been of little practical taxonomic use in this instance. Intra-plant variability in ligule number may be under hormonal control, which may be delicately balanced in hybrid material.

2. EXPERIMENTAL S. AETNENSIS X S. CHRYSANTHEMIFOLIUS

Reciprocal hybridisations were made by rubbing together open capitula of extreme forms of S. aetnensis and S. chrysanthemifolius grown from seed collected from Mt. Etna. These parental plants were designated, respectively, E62:2 and E20:5, details of which are given in Table 15.

Seed set in both parents following cross-pollination was over 90% in every capitulum. Of about 50 plants grown

Table 15

Scores (see Table 13) of F_1 hybrids between Senecio aetnensis (E62:2) and S. chrysanthemifolius (E20:5):

PLANT	SCORE														OTHER CHARACTERS					
	leaf shape	leaf dissection	leaf auricles	glaucosity	hairiness	ligule length	ligule breadth	bract tips	capitulum length	capitulum breadth	achene length	achene colour	achene hairiness	TOTAL SCORE	% pollen stained	pollen variability	ligule variability	scores of sibs	% pollen stained of sibs	altitude of parent plant (metres above sea level)
E20:5	10	10	10	10	10	9	10	7½	8	5	10	10	10	119½	62.8	V	X	113		ca. 50
E62:2	3⅓	0	2½	0	0	2	3	0	3	5	6⅔	10	0	35½	62.6	V	X	34	98.6	ca. 1750
																		39½		
E62:2♀ X E20:5♂	3⅓	6	2½	5	5	5	8	2½	7	6	6⅔	10	5	73	80.9	R	X			
	3⅓	6	7½	5	0	5	8	2½	6	5	8	10	5	71⅓	84.7	R	Y			
	6⅔	7	5	5	0	6	7	2½	6	6	8	10	5	74⅙	83.2	R	X			
	6⅔	6	5	5	0	5	8	2½	6	6	6⅔	10	5	71⅚	89.0	R	X			
	3⅓	7	7½	5	0	5	8	2½	6	5	-	-	-	-	-	-	-			
	6⅔	7	2½	5	5	5	6	2½	6	5	6⅔	10	5	72⅓	-	-	-			
	3⅓	8	5	5	5	5	8	2½	7	5	6⅔	10	5	75½	81.7	R	X			
	3⅓	6	5	5	0	6	7	2½	6	5	-	-	-	-	-	-	X			
	3⅓	6	7½	5	0	5	7	2½	6	5	-	-	-	-	72.9	V	X			
	3⅓	6	7½	5	0	5	7	2½	6	5	8	10	5	70⅓	91.3	R	Y			

- continued -

	leaf sh.	leaf di.	leaf au.	glauc.	hair.	lig. l.	lig. b.	br. tips	cap. l.	cap. b.	ach. l.	ach. col.	ach. hair	TOT. SC.	% poll.	pol. var.	lig. var.
E20:5♀ X E62:2♂	3⅓	6	7½	5	0	5	8	2½	6	5	8	10	5	71⅓	87.8	R	X
	6⅔	6	5	5	0	4	7	2½	6	5	6⅔	10	5	68⅔	85.4	R	X
	6⅔	6	7½	5	0	5	8	2½	6	5	6⅔	10	5	73⅓	73.3	R	X
	6⅔	5	5	5	5	6	8	2½	7	5	6⅔	10	5				
	3⅓	6	7½	5	0	6	8	2½	6	5	6⅔	10	5				
	6⅔	6	2½	5	0	4	6	2½	6	5	6⅔	10	5				
	6⅔	6	7½	5	0	5	8	2½	6	5	8	10	5	74⅓	91.0	R	Y
	6⅔	6	5	5	0	5	-	-	-	-	-	-	-	-	-	-	-
	6⅔	6	5	5	0	5	8	2½	6	5	-	-	-	-	-	-	-
	6⅔	6	7½	5	0	5	-	-	-	-	-	-	-	-	-	-	-

MEANS

	leaf sh.	leaf di.	leaf au.	glauc.	hair.	lig. l.	lig. b.	br. tips	cap. l.	cap. b.	ach. l.	ach. col.	ach. hair	TOT. SC.
E20:5 and E62:2	6.7	5.0	6.3	5.0	5.0	5.5	6.5	3.8	5.5	5.0	8.4	10.0	5.0	77.5
E62:2♀ X E20:5♂	4.3	6.5	5.5	5.0	1.5	5.1	7.4	2.5	6.2	5.3	7.6	10.0	5.0	71.9
E20:5♀ X E62:2♂	6.0	5.9	6.0	5.0	1.0	5.0	8.0	2.5	6.1	5.0	7.3	10.0	5.0	72.8
means	5.2	6.2	5.8	5.0	1.3	5.1	7.7	2.5	6.2	5.2	7.5	10.0	5.0	72.4

Note: R = pollen of regular size; V = pollen of irregular size;
X = ligule number regular; Y = ligule number variable.

from each parent no maternal types were observed, using leaf dissection as the distinguishing criterion. Ten plants from each cross were grown to maturity, and their characteristics are recorded in Table 15.

The F_1 hybrids between E62:2 and E20:5 are slightly variable, but are intermediate between the parents. This indicates that the parents were fairly homozygous for the genes concerned in controlling morphological differences between them; also, these genetic differences are not controlled by single genes, and dominance is absent.

Both of the parents, E62:2 and E20:5 had a much reduced pollen stainability (62.6% and 62.8%, respectively), and were of the class with variable pollen size. Although their hybrids all had a reduced pollen stainability compared with the normal 97 - 100%, they with only one exception were of regular size and had a higher pollen stainability (72.9 - 91.3%) than their parents. A possible interpretation of this situation is that nuclear or cytoplasmic complementation has taken place in the hybrids so that the variable pollen size and high pollen stainability of the parents are not expressed. Alternatively, if the expression of the variable pollen character is environmentally affected (as already suggested) then the hybrids being grown at a different time from their parents may have resulted in it not appearing. Again, observations of pollen mother cell meiosis revealed no abnormalities in the hybrid plants: - five of them were studied.

A more comprehensive programme of crossings between S. aetnensis, S. chrysanthemifolius and the various intermediates (including the British S. squalidus) would be necessary to determine more accurately the relationships between the taxa involved in this complex, but some deductions can be made on the basis of the evidence presented here. It is probable that the character differences between S. aetnensis and S. chrysanthemifolius are determined in most cases by multiple gene control, which in the extremes of each taxon approach homozygosity. The main control of introgression between S. aetnensis and S. chrysanthemifolius in the field is almost certainly altitudinal separation of environmentally adapted genotypes coupled with selection of the hybrid progeny phenotypes.

THE BRITISH SENECIO SQUALIDUS

The British S. squalidus, although polymorphic, falls in every character observed within the morphological range of the Sicilian taxa. Its range is, however, more narrow, and occupies a more or less intermediate position between the extremes of the Sicilian taxa (see Table 16).

The narrow range and intermediate position of the British taxon can be explained as being the result of the introduction of limited biotypes; possibly from a hybrid ("S. incisus") population in Sicily. Substantial genetic depletion may also have occured if many generations were involved between its introduction and eventual escape from cultivation.

Many of the extremes of morphology in the British S. squalidus are only rarely encountered. Some I have never seen in the field, although descriptions are in the literature, or I have examined herbarium specimens (see the Notes for Table 16). These extreme types could be the result of mutation, although they can usually be incorporated within the range of the Sicilian taxa, and this indicates that residual variation and the rare recombination of ancestral characters is a more probable explanation.

The sudden spread of S. squalidus following a century of cultivation in Britain may have been due to catastrophic selection with or without cryptic introgression resulting in plants adapted to British conditions. The rapidity of establishment of the taxon outside of the Botanic Gardens

Table 16

Comparison of the British and Sicilian taxa of Senecio squalidus s l

Character:	Taxon		Comments:
	Sicilian:	British:	
habit	semi-creeping to erect		environmentally controlled
fleshiness of leaves	S. aetnensis often fleshy on Mt. Etna	non-fleshy, but fleshy leaved plants have been recorded in a salt marsh (1)	Sicilian character, at least, is environmentally controlled
leaf dissection (see Figure 4)	A - K	usually I - G, but occasionally dissection as extreme as A can be seen (2); the uncommon variety subinteger Druce has leaves approaching type D (3)	not affected by environment, and continuous range of variation indicates polygenic control
leaf auricles (see Figure 4)	range from large and entire; to nearly absent and much dissected; to absent	usually medium sized and moderately dissected; total range is probably similar to the Sicilian taxon	

- continued -

glaucosity and hairiness of aerial parts	range is from glaucous and glabrous to slightly hairy and non-glaucous	usually slightly hairy and non-glaucous; glaucosity is very rarely met with (4)	not affected by environment
types of trichomes (see Plates in Materials and Methods)	all are very rare in S. aetnensis, and present in S. chrysanthemi-folius	all types are present	glandular trichomes are not apparent macro-scopically; the hirsute character is due to both club and whip trichomes
achene colour	light to dark brown, greenish achenes often present	medium to dark brown, greenish achenes often present	any green colouration is usually restricted to the peripheral (but not necessarily ligulate) florets
achene length	2.1 - 4.0 mm.	2.0 - 2.6 mm.	
achene hairi-ness	range from glabrous to hairy	nearly always hairy but the uncommon var. leiocarpus Druce, with glabrous achenes has been recorded on several occasions (5)	hairs are always in ~~groove~~ grooves of achenes
persistence of achenes	achenes tend to persist on S. aet-nensis in Sicily	varies in field	environmentally controlled, at least in Sicily

- continued -

capitulum size (length x breadth)	range from 5.5 x 3.5 to 9.5 x 7.5 mm.	range from 6.0 x 4.0 to 9.0 x 7.0 mm.	
inner involucral bract tip colour	range from colour-less to dense black	always more or less dense black	blackness sometimes disappears in hybrid material (see later text)
ligule size (length x breadth)	range from 4.5 x 2.0 to 15.5 x 5.0 mm.	range from 9.2 x 2.0 mm. to 13.2 x 4.2 mm.; plants outside of this range have been recorded (6)	genetics of the situation are discussed on pp. 73 + 118-9
ligule number per capitulum	(7-) 8 (-9-12-) 13 (-15)	(8-) 13 (-22); numbers exceeding 15 are very rare	Sicilian plants probably represent 8 and 13 ligule taxa; the character in all taxa shows intra-plant variation

Notes on Table 16:

1. Salt marsh, Llandudno, Denbigh: 1958 and 1959 (LIVU).

2. Near Windsor, Berkshire: 1966, my own observations.

3. S. squalidus with more or less entire leaves has been recorded on numerous occasions. Druce described plants such as these as forma subinteger, and tested its constancy when grown for more than one generation (Rep. Bot. Soc. and Exch. Club for 1928: 914). Herbarium records are given below, but as the character is not sharply delimited, a degree of latitude is required in its determination: Oxford: 1870, 1975 (MANCH); 1885, 1943 (BM); 1919 (CGE); 1928 (OXF). Cork: several specimens 1880 - 1900 (DBN). Cardiff: 1902 (BM and LIVU). Didcot, Berks.: 1904 (BM). Bristol: 1912 (BRISTM). Delamere, Cheshire: 1912 (LIV). Northwich, Cheshire: 1918 (MANCH). Exmouth, Devon: 1953 (CGE). Holborn, London: 1950 (OXF). Doncaster: 1956 (CGE).

4. The same plant (and its progeny) as in note 2: - a slight glaucosity, removable by rubbing, was apparent on the leaves.

5. S. squalidus plants with glabrous achenes were first described from the Oxford/Didcot/Reading area by Druce as var. leiocarpus (Journ. Bot. 45 N.S.:66-67 (1906)). Herbarium records are: Newbury, Berks.: 1904 (OXF); Didcot, Berks.: 1904 (OXF, CGE, LIVU); Linley, Salop.: 1906 (MANCH, CGE, LIVU).

6. In 1867 Thistleton Dyer described var. parviflorus from Oxford, with ligules shorter than normal (Rep. Bot. Soc. and Exch. Club for 1867). Several other records of "S. squalidus X S. vulgaris", etc. might have been placed into this category if it had been better known, but I believe that a substantial number of such plants may be fertile S. squalidus X S. vulgaris intermediates of the type discussed later. Apart from the progeny of the eligulate S. squalidus refered to below, I have seen only one plant which could have been a short liguled S. squalidus. This was a depauperated plant from St. Catherine's Dock, east London (found in 1968), which in cultivation produced ligules of a mean length of 0.6 mm. (they were about 7 mm. in the wild). The relatively short length of the fully expressed ligules of this plant (the range for S. squalidus is usually 9 - 13 mm.) may indicate a genetic component in the reduction in ligule length. Of eligulate plants, three have been reported to me. One, a plant supplied to me by Dr. K. Goodway of Keele University, is reported on in greater length later in the text (pp.118-9). In addition D.H. Kent (personal communication) reported solitary specimens on a wall near Kew Gardens in 1962, and at Alperton, Middlesex in 1965. Possibly these were segregants from S. squalidus X S. vulgaris, as are described later, but Dr. Goodway's specimen is definitely S. squalidus, with 2n = 20 (my own observation).

might indicate that a fundamental change had taken place. The lack of any recognisable characters from neighbouring taxa reduces the likelihood of introgression having been responsible for this. The change was therefore more likely to have been the result of mutation.

A further explanation is required for the success of S. squalidus in Britain. It is a well known argument that isolated taxa of self-incompatible species selectively tend towards self-compatibility (Stebbins, 1957; Baker, 1959). In addition, Darlington (1963) quotes two examples of limited introductions into Britain of horticultural species which have subsequently given rise to variable populations due to genetic changes in their breeding systems rather than to hybridisation with other taxa. In Lathyrus odoratus the genetic control of breeding has effected a change from outbreeding to inbreeding. In Primula sinensis many cultivars are now only of the pin-styled type, which is capable of a slight degree of self-pollination, - the "wild" populations are composed of plants with both pin and thrum styles, as determined by opposing alleles, which usually ensures outbreeding.

S. squalidus possesses an efficient self-incompatibility system, and the selective forces of about a century's cultivation on what must have been small populations may have resulted in a tendency towards self-compatibility. Little of any tendency towards self-compatibility can now be seen in the British S. squalidus, but reference to

Appendix Table 2 shows that different degrees in the occurrence of maternal-type offspring can be obtained when hybridisations and self-pollinations are attempted with the various taxa of S. squalidus. The data in Appendix Table 2 is drawn from attempts to produce hybrid material using emasculated and intact capitula. It suffers from the consequent lack of appreciation of potentially differing incompatibility reactions, and no attempt was made to assess whether selfing or agamospermy was taking place. If it is assumed that selfing has been taking place, then it appears that the British S. squalidus can give a weaker self-incompatibility reaction than is apparent in the Sicilian plants. It is possible, therefore, that a genetically controlled change in breeding behaviour could have caused or aided the sudden success of S. squalidus in Britain. The variability shown in both the present day plants and the old herbarium specimens of the taxon indicate that this postulated reduction in self-incompatibility was not complete, for the tendencies towards homozygosity and reduction in variability associated with inbreeding have not taken place. What is more probable is that occasional leakage in the self-incompatibility system allowed the establishment of self-maintaining populations of the taxon, but also allowed a considerable degree of heterozygosity to persist. The overall reduction in self-incompatibility may have been due to one or a few mutations of incompatibility alleles, although the data in Appendix Table 2 indicate that a

generalised reduction in self-incompatibility has taken place at the individual rather than the population level, and suggest a change in the overall expression of the incompatibility system. A comparison can be drawn with the situation in Brassica oleracea (Watts, 1965), where intensive selection over a prolonged period has resulted in varying degrees of reduction in the self-incompatibility system.

THE TAXONOMY OF SENECIO SQUALIDUS

Throughout this discussion of Senecio aetnensis and S. chrysanthemifolius they have been treated as separate taxa which have become partially sympatric, with the resulting hybridisation and genic introgression. Another possibility exists: that the two taxa are in the process of speciation from a single taxon into lowland and montane ecospecies. Evidence for either point of view is fragmentary. The advent of agricultural Man had a considerable affect upon the Mediterranean ecosystem, with the breakdown of certain vegetation types as a result of domestic animal grazing. Thus, the introduction of large numbers of sheep and goats onto Mt. Etna may have resulted in the removal of the natural deciduous woodland barrier between S. aetnensis in the montane zone and S. chrysanth--emifolius in the lowland areas. It is difficult to choose the more likely of these hypotheses. Table 12 can be interpreted as evidence for the selection of novel characters as readily as it can be viewed as evidence for the selection of introgressed characters. In addition, the relative lack of reproductive isolation or hybrid sterility between S. aetnensis and S. chrysanthemifolius (Figures 8 and 9), although not offering conclusive support of the recent monophyletic origin of these taxa, at least do not support their "polyphyletic" origin.

The present state of S. aetnensis and S. chrysanthem--ifolius is that of two selectively maintained taxa sharing

a common gene pool. They are fairly distinct, but overlap morphologically, ecologically, and geographically. This present state is the only criterion to be considered, both in their taxonomic treatment, and in their future adaptation.

At least three taxa are directly involved in the S. squalidus complex: two in Sicily and South Italy, and one in Britain. The genetic continuity between the two Sicilian taxa has been demonstrated, but a morphological discontinuity appears to be fairly strongly maintained in the field. The great majority of specimens in Sicily fall more or less clearly into the two taxa, aetnensis and chrysanthemifolius. These groups demand recognition at least at the subspecific level.

The British taxon corresponds most closely to the hybrid Sicilian material. These hybrid swarms formed between the two Sicilian taxa do not, however, merit taxonomic ranking in the same sense as does the British taxon. The British taxon, in view of its widespread and distinct geographical distribution and circumscribed morphology should be treated as a separate and third species or subspecies of equal status with aetnensis and chrysanthemifolius.

The situation is confused by the close similarities between the British taxon and the French S. gallicus Chaix. (Harland, 1954) and the Central European S. rupestris W.&K. (Walters, 1963). There is no evidence to suggest that these species have contributed to the British taxon, or that they own a directly common origin. Both Harland and Walters

suggested that their respective taxa might be combined with the British S. squalidus on the basis of their cross fertility and morphological similarity. Additionally, of the few other diploid polycarpic Annui to have been studied, the morphologically distinct S. rodriguezii Willk. forms fertile hybrids with S. squalidus (see pp. 18-19).

The incorporation of all taxa into a single species may reflect the phylogenetic situation accurately; but the use of subspecies would be necessary, and taxa such as rodriguezii on morphological grounds are too distinct to merit this treatment, despite requiring some incorporation into the taxonomic scheme. Alternatively, all taxa may be treated as distinct species: this involves the minimum revision of nomenclature, but is probably not justifiable on morphological grounds. The most convenient solution, and the one which I favour, is to treat these taxa as a species complex. In this case the group would be refered to as the Senecio squalidus aggregate, this consisting of:

S. squalidus L. in the British Isles and parts of continental N.W. Europe (see footnote).

S. aetnensis Jan. in the montane Etnan region of Sicily.

S. chrysanthemifolius Poir. in lowland Sicily and southern Italy.

Included in the species aggregate would be S. rupestris W.& K.

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footnote: Senecio squalidus, almost certainly of British origin, has been reported as established in Northern Ireland (Boyd, 1965); Denmark (Pederson, 1961); northern France (Lousley, 1957); and the Channel Islands (McClintock, 1959).

(Central Europe), S. gallicus Chaix.(France and Spain), and S. rodriguezii Willk. (Balearic Islands) on the evidence already suggested. Other species, such as the north-west Mediterranean S. crassifolius Willd. and the west Mediterranean S. leucanthemifolius Poir. may be included in the aggregate as they are studied further.

The status of the hybrid swarms in Sicily between S. aetnensis and S. chrysanthemifolius should be maintained as S. incisus Presl., with the clarification that they should be refered to as S. X incisus (= S. aetnensis X chrysanthemifolius).

SENECIO VULGARIS

INTRODUCTION TO THE SPECIES

Senecio vulgaris Linnaeus (Sp. Pl. 1753: 867) is a monocarpic weed, with a rapid and prolific life cycle. It is native and often abundant throughout the Temperate regions of the Old World. In addition, it has been widely introduced by Man to the extent that it now occurs commonly in Australia and North America, and has been recorded in many other parts of the World.

S. vulgaris is well adapted to be a weed by its breeding habit. The species is self-compatible, and the floral ontogeny (see Appendix, pp. 246-253) ensures self-pollination if cross-pollination does not occur. The capitula are small and insignificant, even in the ligulate types, and although functional nectaries are present (Knuth, 1908; Percival, 1961), insect pollination is minimal. The infrequency of cross pollination is indicated by the rarity of hybrids (see later discussion on ligulate/eligulate hybrids on pp. 90 - 91), and by field observations of the scarcity of insect visitors to the plants. Most insect visitors are small Diptera.

The rapid rate of seed production, coupled with the inbreeding habit results in the proliferation of similar genotypes and the development of populations consisting of one or more distinct biotypes potentially sharing in a common gene pool. Under conditions where the species colonises newly opened, favourable habitats (such as in

arable farmland) selection for phenotypic performance except as is directly related to reproductive capacity must be negligible. Where selection is effective, however, the inbreeding habit must result in the disproportionate success of certain genotypes. R. Abbott and J. Antonovics (unpublished data) investigated populations of S. vulgaris from stable high and low nutrient status habitats, which also differed in their degree of climatic exposure. Despite the close proximity of certain of their populations (as little as 100 metres) they found that each population was distinct, and was genetically fairly uniform and precise in its adaptation to the utilisation of available nutrients. The populations also differed in their genetically determined morphological characteristics. Abbott and Antonovics also noted that despite the prevalent inbreeding of their populations, a slight degree of variability occurred in the offspring of each plant. They suggested that this was due to occasional outcrossing, indicating the participation of these populations in a larger gene pool.

Essentially similar results were obtained by Kumler (1969) with two races of the very similar species S. sylvaticus which have become morphologically and edaphically adapted to different nutrient states in coastal regions of Oregon, North America. This adaptation is of fairly recent origin, the species having spread to Oregon from California, where it was first recorded in the 1920's (Robbins et al, 1951; Chilcote, 1962).

Bateson (1887) reported heterotic vigour in hybrids obtained by crossing different lines of S. vulgaris. His measurements were of increases in height, fresh weight, earliness of flowering, and seed set and germination in the hybrids as compared with the self produced offspring. He was, however, only working with a very small sample, and his parental material apparently had a degree of self-sterility (selfing led to 63% seed set, crossing to 91%). In the absence of further information concerning this material, it must be assumed that it was atypical. Heterosis is not to be expected in successful inbreeding species. The tendency is towards increasing homozygosity for genes not selectively maintained as heterozygotes. Successful gene combinations must be internally balanced, this condition being selectively maintained; this is in contrast to outbreeders, where selection will favour relational balance of genes recombined at each generation (Mather, 1943). Two other workers in this field (Plack, 1952; and V.A. Matthews, personal communication), as well as myself, who have hybridised different strains of groundsel have failed to find heterosis. Trow (1912) in his genetic analysis of groundsel obtained his hybrids by screening the results of his cross-pollinations for positively heterotic (and therefore hybrid) individuals. This method may be of use with certain races in certain environments. Heterosis in S. vulgaris must not be regarded as a common phenomenon. Consequently, inbreeding depression has yet to be demonstrated in S. vulgaris, and

may reasonably be expected not to occur as a general characteristic of the species.

Distinct races of the species have been recognised by a number of authorities. Harland (1954) and several workers associated with him investigated many races of groundsel from all over the World, and noted the relative lack of morphological differences between these races. They did, however, describe notable differences in *in vitro* growth rates of excised roots (Street, in Harland, 1954). Races such as these have seldom been given taxonomic recognition, due to the very minor nature of the morphological differences between them. In *S. vulgaris* most of the small genetic differences between races are also obscured by very marked phenotypic plasticity, and are therefore not given taxonomic recognition. The ligulate varieties of the species have, however, nearly always been recognised taxonomically, and these are discussed in detail later. A number of other biotypes have been named. Trow (1909, 1912) described several "species" of groundsel, all differing from one another by several genetically determined characters. His treatment has subsequently been criticised (Wilmott, 1925, 1949) because of the trivial and impermanent nature of the differences between these taxa. Trow was, however, well aware of the breeding system in groundsel and its consequences. If he had referred to his "species" as microspecies, he would have essentially been in line with present-day taxonomic treatment of such taxa.

THE LIGULATE VARIETIES OF SENECIO VULGARIS

The ligulate varieties of S. vulgaris have commonly been refered to en bloc as var. radiatus Koch. (Allen, 1967). This is the name used in the current British Flora (Clapham, Tutin and Warburg, 1962). The name has also been, and still is in common usage in Britain and Europe. The name was originally applied to ligulate coastal forms of the species (as S. vulgaris var. radiatus Koch. Syn. Fl. Germ. Ed. 1: 386 (1837)), but has generally been extended to include all other ligulate forms. Allen (1967) clarified the situation by explaining that the ligulate coastal variety should be refered to as var. denticulatus (O.F. Muell.) Hyland (from Mueller's original inclusion of the race in S. sylvaticus), and the non-coastal ligulate races as var. hibernicus Syme. Alternatively, if a single taxon, including all ligulate races is to be recognised at the formal level, he pointed out that the correct name would be f. radiatus Hegi. Allen's paper prompted the re-assortment of the records of the ligulate varieties into denticulatus and hibernicus in preparing the maps in the Critical Supplement to the Atlas of the British Flora (Perring, 1968). Sell (1967; and in the Critical Supplement) elevated denticulatus (O.F. Muell.) P.D. Sell to subspecific level in view of its wide geographic range, and reduced hibernicus to formal status as f. ligulatus D.E. Allen.

SENECIO VULGARIS VAR. HIBERNICUS

Allen (1967) pointed out that the coastal ligulate S. vulgaris was recognised as S. sylvaticus var. denticulatus O.F. Muell., and S. vulgaris var. radiatus Koch. (some years before the inland ligulate type was first described) by German authors. The tendency ensued for all ligulate S. vulgaris races to be referred to as var. radiatus Koch.. Syme (1875), when describing var. hibernicus showed that this inland taxon differed from var. denticulatus in being more profusely branched, less hairy, with more dissected leaves, and larger, spreading ligules. As Allen (1967) said "these inland rayed variants are so conspicuous that it is difficult to believe earlier botanists would have failed to mention them, had they known of them". Allen suggested that this may have been due to their slow establishment, either as very rare mutants, or as stray alien ammigrants, possibly from south or east Europe, or Asia.

Syme's (1875) description of the variety was from material growing profusely around Cork. The first British record was, however, from Oxford in 1832 (LIVU). Before the end of the nineteenth century the variety was present in four areas: southern Ireland (spreading from the Cork area); the Oxford area; the Bristol/Cardiff area; and north-west Wales and Cheshire. The superficial inference was obvious: - this was an introduced taxon, with its distribution based around its ports of introduction (Cork, Avonmouth, Cardiff, and Liverpool), its presence around Oxford being the result

of chance introduction. The tendency to record all ligulate S. vulgaris as var. radiatus increased the acceptability of this hypothesis, due to the coastal distribution of var. denticulatus. These coastal ligulate races were recorded on the Lancashire dunes and on the south coast of Devon. Haskell (1954) propounded this theory, and also suggested that, on the basis of this distribution, the variety might be physiologically better adapted to the warmer, wetter climate of the west of the British Isles. This has been the generally accepted theory up until the present time.

The close affinities of var. hibernicus with the eligulate S. vulgaris were recognised by Trow (1912). He, in describing several morphologically different races of S. vulgaris, included one inland taxon as "S. erectus", which could be either ligulate or eligulate. "S. erectus" was said to have many, rather short and stout internodes and an erect, straight stem. The leaves were deeply pinnatifid or pinnatisect. As is described later (pp. 90 - 98), inheritance of this ligulate character in both Trow's "S. erectus" and his "S. lanuginosus" (≡ S. vulgaris var. denticulatus) followed the normal disomic, monogenic, Mendelian pattern: the heterozygous individuals being distinguishable because of incomplete dominance of the alleles involved. One more of Trow's "species" has subsequently been described as occuring naturally in both ligulate and eligulate forms (D.P. Young, personal communication; and Allen, 1967). This is "S. multicaulis",

characterised by its production of many branches from the basal axils. Trow also noted that the ligulate character could be transferred into several other recognisable morphological races of S. vulgaris by hybridisation.

There have been suggestions that the ligulate character in S. vulgaris may have been the product of gene flow from S. squalidus, or that it was the direct hybrid of these two species. These suggestions were made in the period around the time of Syme's description of var. hibernicus (see the footnote). The summary of these discussions is that the idea that var. hibernicus was the direct hybrid between these two species only went out of favour as Syme and others (footnote) established that var. hibernicus was fully fertile, and came true from seed, and that the true hybrid S. X baxteri (Druce, 1892) was sterile, although the two closely resembled each other.

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Discussion of the status of Senecio vulgaris var. hibernicus took place in the following:

Rep. Bot. Soc. and Exch. Club for 1872-4:27; 1874-5; 1875: 19; 1876:22; 1879:15; 1887:184; 1891:337; 1892:374; 1903; 1906:227; 1910:568; 1915:352;

Rep. Watson. Bot. Exch. Club for 1901-2:15; 1912-13:395.

Journ. Bot. 2 N.S.:119 (1873); 7 N.S.:252 (1878).

Irish Naturalist 6:300 (1897); 9:245 (1900).

Participants in these discussions included:

R.A. Phillips, F.W. Burbidge, C.G. Druce, H.J. Riddelsdell, E.S. Marshall, A. Ley, W.O. Focke, J.T. Boswell, C.E. Moss, A.H. Trow, W. Hodge, H.C. Watson, J. Carroll, T.R. Archer Briggs, A.B. Jackson, and B. Syme.

Since the time of the original controversy regarding the status and origin of var. hibernicus, the possibility that S. vulgaris may have obtained the ligulate character from S. squalidus has seldom been suggested. This was probably due to the rapid spread of both taxa to the extent that they became familiar rather than novel plants to botanists and hence less subject to investigation and speculation. I have been able to find only one recent reference to this possible relationship between the two species, this being Harland's (1954) indication that attempts would be made to back-cross the hybrid S. X baxteri into S. vulgaris in order to ascertain if the ligulate character of the latter species "was an indication of the common ancestry of these two species". The results, if any, of this experiment have never been published. This investigation was prompted by the description and artificial synthesis of the allohexaploid hybrid of S. vulgaris and S. squalidus, - S. cambrensis (Rosser, 1955), which is discussed in greater detail later.

The F_1 hybrid between S. vulgaris (2n = 40) and S. squalidus (2n = 20) should be triploid (2n = 30). Apart from Harland's (1954) studies of this hybrid and of S. cambrensis (2n = 60), no previous analysis has been made of intermediate and anomalous plants of this group from the aspect of cytology, and no suggestion has hitherto been made of a mechanism of gene flow between the two species. The rest of this Chapter deals mainly with different aspects of the hypothesis that introgression takes place from S. squalidus into S. vulgaris.

GENETIC ANALYSIS OF THE LIGULATE CHARACTER IN SENECIO VULGARIS VAR. HIBERNICUS

S. vulgaris plants with very small ligules, in mixed populations of eligulate and ligulate plants have been recorded on a number of occasions (see Table 17), and in my experience they are fairly common in such populations, whether natural or cultivated, where insect pollination is possible.

These individuals with very small ligules were interpreted as being heterozygous for the ligulate character by Trow (1912) and Plack(1952), who assessed the segregation ratios of the self-produced progeny of these plants. Their results are summarised and analysed in Table 18. Trow suggested that these results could be interpreted in terms of partial dominance of the ligulate gene (L) over the eligulate gene (+). Plack's results support this interpretation, although she does record that some variation occured in ligule lengths in both LL and L+ classes, the former ranging from 4.1 - 5.3 mm., and the latter from 1.0 - 1.8 mm.. In both cases this variation appeared to follow a normal distribution, presumably being the result of natural morphogenetic variability.

I repeated these experiments using two strains derived from populations of mixed eligulate/ligulate individuals and my results are included in Table 18. One population orig--inated from weeds in the Cambridge Botanic Gardens, and the other from a roadside population in Brymbo, near Wrexham,

Table 17

Recordings of spontaneously produced intermediate ligulate Senecio vulgaris in the British Isles:

reference	date	locality	comments
Trow (1912)	1904	cult., ex Cardiff, Glamorgan	growing with the ligulate and eligulate forms
Riddelsdell (1912)	1912	Llandaff, Glamorgan	growing with the ligulate form
Stephenson (1936 and 1946)	1936 and 1946	cult., ex Teignmouth, Devon	
Plack (1952)	1951	Mt. Batten, Plymouth, Devon	a single population of 673 eligulate, 267 ligulate and 41 intermediate
Young (1952)	1952	cult., ex Flintshire?	
Heslop-Harrison (1957)	1957	Cassop, Co. Durham	a mixed population with the intermediates showing a range of form
Crisp, unpublished	1967	Cambridge Botanic Gardens	growing with the ligulate and eligulate forms
	1967	Brymbo, near Wrexham, Denbigh	common in mixed population of ligulate and eligulate forms
	1968	cult., ex several localities	common in mixed populations established from experimental material

Note: The incidence of heterozygotes in these populations is only a measure of the maximum possible hybridisation which could have taken place between ligulate and eligulate plants in the preceeding generation. Even a single generation of inbreeding following the appearance of a heterozygote would result in a halving of the relative incidence of the heterozygote, due to segregation of the homozygotes, and by the fourth generation of inbreeding the theoretical ratio of heterozygous plants (L+) to homozygous plants (LL) will be less than that shown by the Mt. Batten population described above (that is 11.8% as opposed to 13.3%).

Table 18

Inheritance of the ligulate character in Senecio vulgaris, a summary of published and unpublished results (subjected to a X^2 test):

LL = ligulate; L+ = intermediate; ++ = eligulate

source	parent and treatment	total number of seedlings	total number flowered	progeny LL	L+	++	likelihood of 1:2:1 ratio, P =
Trow (1912)	LL selfed	36	8	8	0	0	
		119	116	116	0	0	
		?	5	5	0	0	
		74	74	74	0	0	
	LL natural	13	13	13	0	0	
		660	617	616	1	0	
	++ natural	439	439	0	0	439	
	L+ natural	491	449	114	226	109	> 0.9
	L+ selfed	?	503	117	270	116	> 0.4
		?	108	23	46	39	> 0.025
		?	461	122	218	121	> 0.5
		?	234	53	115	66	> 0.4
		?	83	26	35	22	> 0.3
		?*	92	26	41	25	> 0.6
		?*	88	23	43	22	> 0.9
		?*	92	23	52	17	> 0.3
		?*	202	44	109	49	> 0.4
		?*	48	11	25	12	> 0.9
		?*	97	20	39	38	> 0.005
Plack (1952)	L+ selfed	325	244	72	111	61	> 0.2
		424	230	70	90	70	> 0.004
		?	281	74	140	67	> 0.7
		?	209	47	112	50	> 0.7
		?	201	52	88	61	> 0.1
		246	46	17	19	10	> 0.1
		99	12	3	7	2	(> 0.8)
		174	13	5	5	3	(> 0.5)
		75	3	2	1	0	(> 0.2)
		75	21	5	12	4	(> 0.8)
		24	5	2	2	1	(> 0.7)
		200	153	33	85	35	> 0.3
		250	219	53	100	66	> 0.1
Crisp	L+ selfed	152	133	31	67	35	> 0.8
		152	118	32	59	27	> 0.3
	LL selfed	76	72	70	0	2	
		76	69	69	0	0	
	++ selfed	76	71	0	0	71	
		76	70	0	0	70	

Trow analysed both var. hibernicus (as S. erectus radiatus) and ssp. denticulatus (as S. lanuginosus radiatus), - the latter taxon is indicated in the Table by an asterisk (*).

Denbighshire.

Plants of these two strains were grown and individuals of the three types, - ++, L+, and LL were selected. Capitula that had already opened were removed, and each plant was placed in isolated conditions where no cross pollination was possible. Autogamous seed set was in every case over 95%, and testings of germination indicated that over 99% of this seed was viable and readily germinated. Seed was collected and sown two weeks later in pans. Plants from the seed pans were pricked out into multi-pots. Care was taken so that no unconscious selection was made, and the seed pans were kept for several months to check that no subsequent germination took place.

1. THE CAMBRIDGE STRAIN

Progeny from the eligulate and ligulate (++ and LL) plants both bred 100% true to the parental type. The products of the intermediate (L+) plant gave a fairly uniform production of the three types during the whole course of recording, so that at any stage a more or less 1:2:1 ratio could be recorded (see Figure 10). The final ratio of 35:67:31 was very close to the expected 1:2:1 ratio ($P => 0.8$).

2. THE BRYMBO STRAIN

In this case, the end product was again very near to a 1:2:1 ratio (32:59:27, $P => 0.3$) when 70.8% of the plants had flowered - the rest having succumbed to mildew. However, during the course of the recording considerable deviation from the 1:2:1 ratio was found (Figure 10), and a

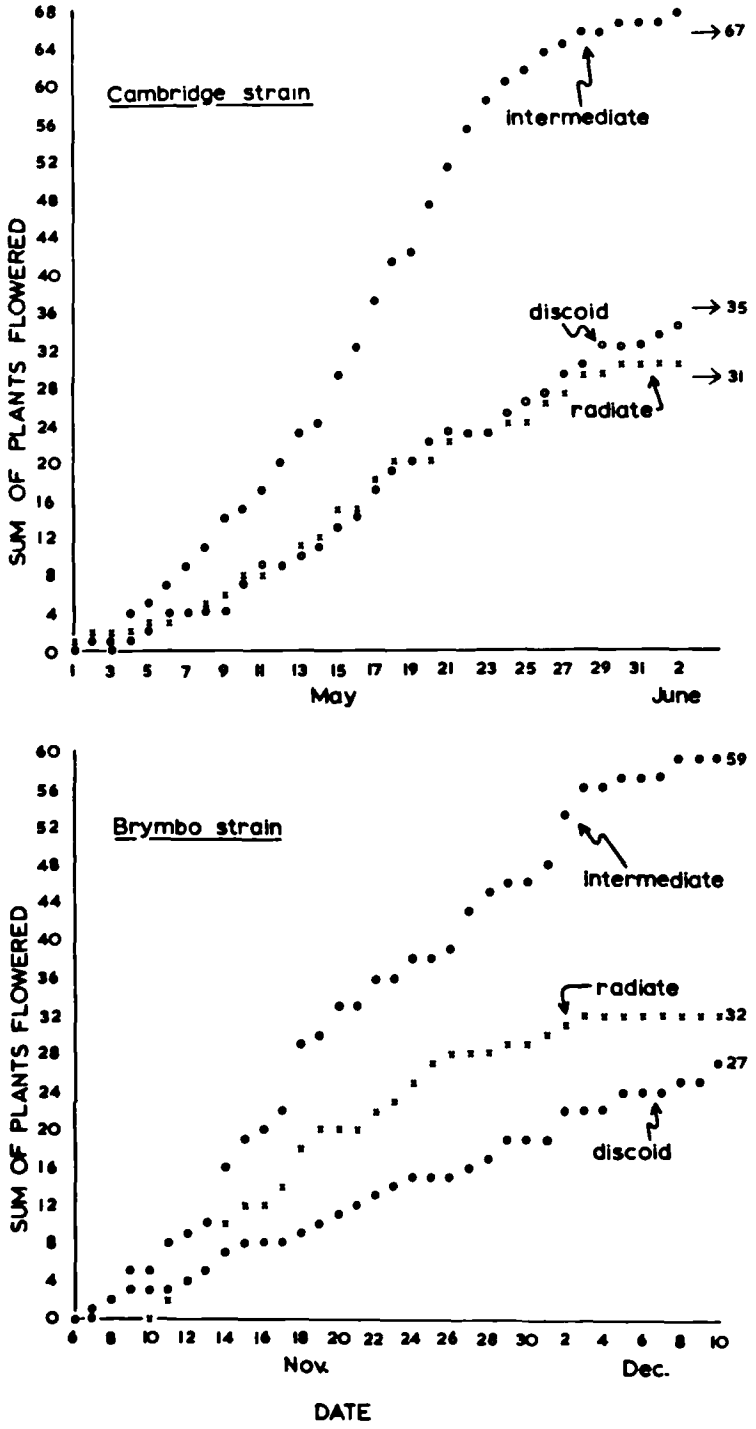


FIGURE 10

Segregation of the radiate character in the autogamously produced offspring of short rayed individuals of Senecio vulgaris var hibernicus

fortuitous termination of the observations would have given anomalous results. This is worth mentioning because, as reference to Table 18 shows, in many cases Trow's and Plack's ratios were based only on a small proportion of their original sample. This indicates that previous genetic analysis of the ligulate character has for the most part been performed on populations with the same behaviour as my Cambridge strain. Some of their results, however, show resemblences to my Brymbo strain, and in one of these cases were based on only 54.2% of the original sample.

Additionally, variation in ligule length in the intermediate (L+) and ligulate (LL) classes of the Brymbo strain (see Table 19):

Table 19 Ligule dimensions of segregants of Senecio vulgaris var. hibernicus:

ligule lengths ± 2S.E. (in mm.)

	heterozygous ligulate (L+)	homozygous ligulate (LL)	super-ligulate
Cambridge strain	1.8 ± 0.1	4.2 ± 0.1	-
Brymbo strain	1.9 ± 0.2	4.1 ± 0.3	6.3 ± 0.3

Note: Measurements are of 20 ligules from a minimum of six plants of each type, except in the case of the super-ligulate plants (refered to below) of which only two were available.

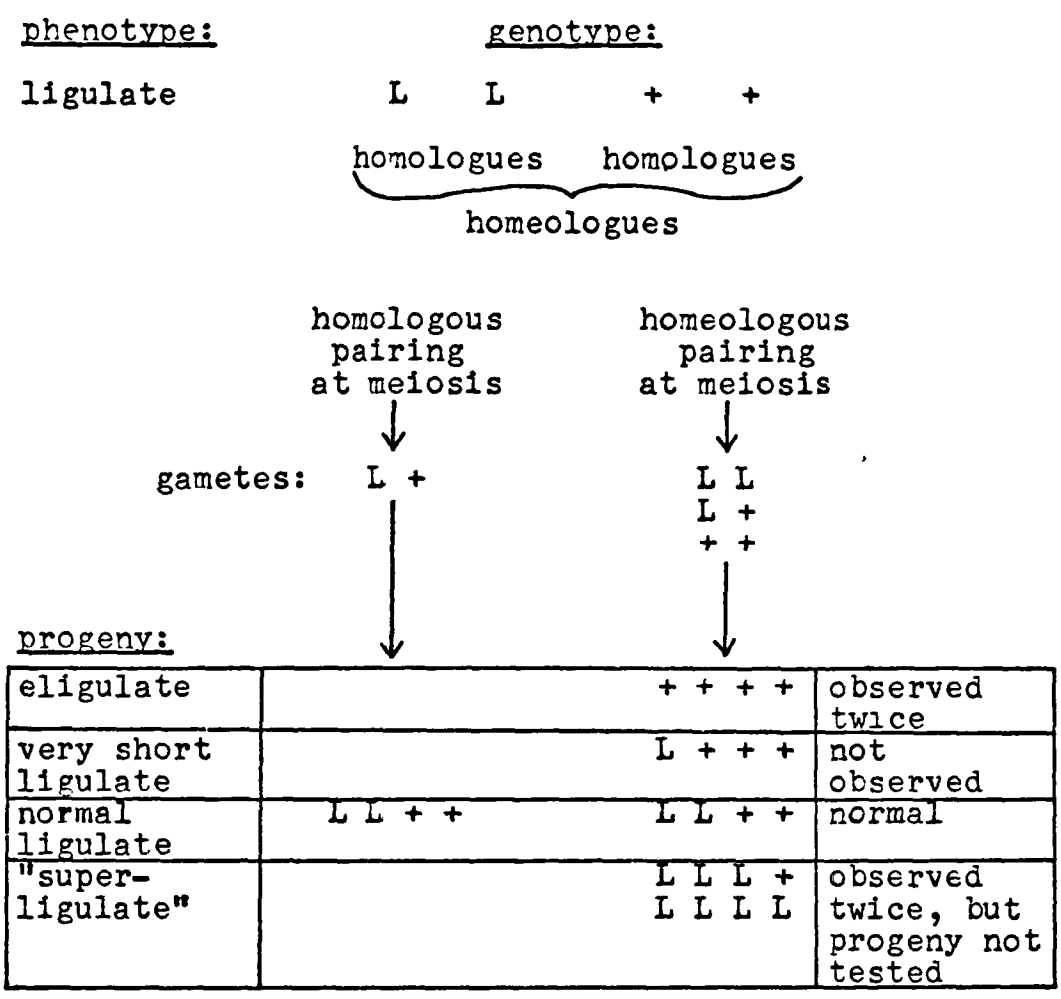
It appears probable, therefore, that the Brymbo strain is less genetically uniform than the Cambridge strain in its background effects on the ligulate gene; and also that there is possible linkage between lateness of flowering and the eligulate gene when it is homozygous in the Brymbo strain.

In common with the Cambridge strain, the Brymbo strain eligulate (++) progeny bred true to type. Progeny of the ligulate (LL) Brymbo plant, however, consisted of 70 parental types and two eligulate plants. These two plants were sickly and late in flowering. I consider it highly unlikely that these were the products of experimental error, and the fact that they were not intermediate (L+) indicated that they were probably not the result of accidental outcrossing. It is relevant here to consider two other anomalous plants which subsequently arose from the Brymbo strain. These plants were large, erect and much branched, with large leaves (see Figure 13) and large ligules (see Table 19). Chromosome trisomy was ruled out by the plants having the normal tetraploid chromosome number of 2n = 40, and by their regular meiosis. Pollen diameters and stainabilities, and seed sizes and fertilities were the same as in the other members of the Brymbo strain.

My suggestion is that S. vulgaris var. hibernicus is a product of introgression from S. squalidus (2n = 20) into S. vulgaris (2n = 40). It will be shown that the early intermediates in this introgression sequence show multigenic, and possibly tetrasomic inheritance of the ligulate character, as well as some quadrivalent formation at pollen mother cell meiosis. These phenomena offer an explanation for the apparently anomalous segregation shown by the Brymbo strain. The results can be explained in terms of occasional pairing of homeologous chromosomes in this strain, as is outlined in Figure 11.

Figure 11

Products of homologous and homeologous chromosome pairing in Senecio vulgaris var. hibernicus:



eligulate		+ + + +	observed twice
very short ligulate		L + + +	not observed
normal ligulate	L L + +	L L + +	normal
"super-ligulate"		L L L + L L L L	observed twice, but progeny not tested

The relatively recent hybrid origin of the Brymbo strain is also consistent with the lack of homozygosity of the genetic background affecting the ligule gene, as already mentioned. Unfortunately, no indications of meiotic disorders (such as univalents, bridges, etc.) could be found in this strain to support the hypothesis of homeologous pairing, which, on the basis of the frequency of anomalous plants appearing, must be fairly rare events. Their pollen

fertility is less than that of the Cambridge strain, and pollen sizes are more variable (see Table 20), but these could as well be due to other causes than meiotic abnormalities.

Table 20 Pollen and seed sizes, pollen stainability, and seed set in two different strains of Senecio vulgaris var. hibernicus:

	POLLEN		SEED	
	% stained 2S.E.	diameter 2S.E.(μ)	% set 2S.E.	length 2S.E.(mm.)
Cambridge strain	98.7 ± 0.2	25.8 ± 0.4	97.3 ± 0.2	2.1 ± 0.1
Brymbo strain	94.8 ± 0.5	27.2 ± 0.4	93.2 ± 0.6	2.2 ± 0.2

Note: Pollen stainabilities are based on counts in excess of 400 grains; pollen dimeters on at least 50 measured stained grains. Seed set is based on the complete seed complement of at least 3 capitula; seed length on measurements of at least 20 randomly selected set seeds. In all measurements, between 3 and 10 plants of each strain were involved.

To summarise: in most cases the ligulate character in S. vulgaris var. hibernicus performs as if it were under the control of a single major gene with partial dominance operating. In certain cases the behaviour of this gene indicates that it may be linked with other characters, or that there may be more copies of the gene present in a cryptic state.

HISTORICAL AND GEOGRAPHICAL EVIDENCE FOR THE CORRELATED SPREAD OF SENECIO VULGARIS VAR. HIBERNICUS AND S. SQUALIDUS.

Both S. squalidus and S. vulgaris var. hibernicus have been fairly well recorded in the literature and in herbaria, for both were novel and conspicuous taxa, usually occuring in habitats in close proximity to well populated areas. Apart from the recording of all ligulate S. vulgaris races as "var. radiatus", and a slight tendency to confuse S. squalidus with S. aquaticus and, particularly, with S. erucifolius, the spread of the two taxa has been fairly reliably recorded in the literature. My search for intermediates, however, demanded that herbaria should be consulted, and therefore most of these records have been checked, and the maps given in Figure 21 refer only to those records substantiated by me or by others familiar with these plants (see Appendix Tables 11 and 12).

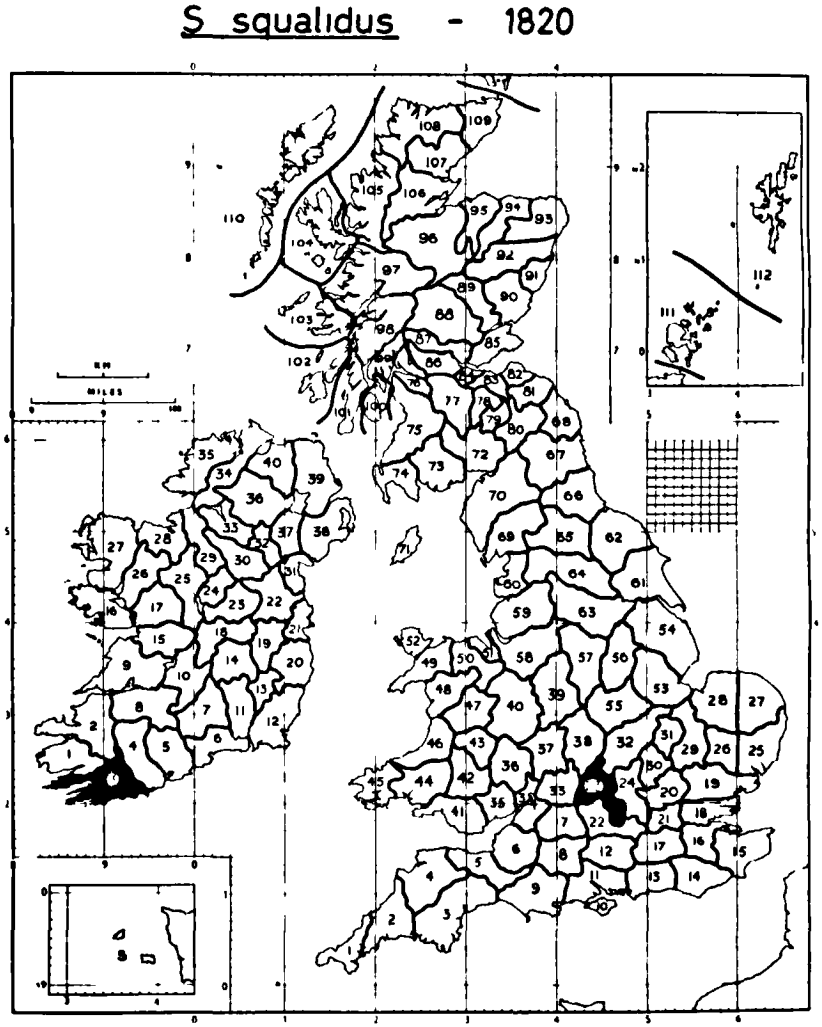
An investigation of the spread of these two taxa outside of Britain is beyond the capacity of this type of project, calling as it does for first hand investigation of large quantities of herbarium material and of minor botanical publications.

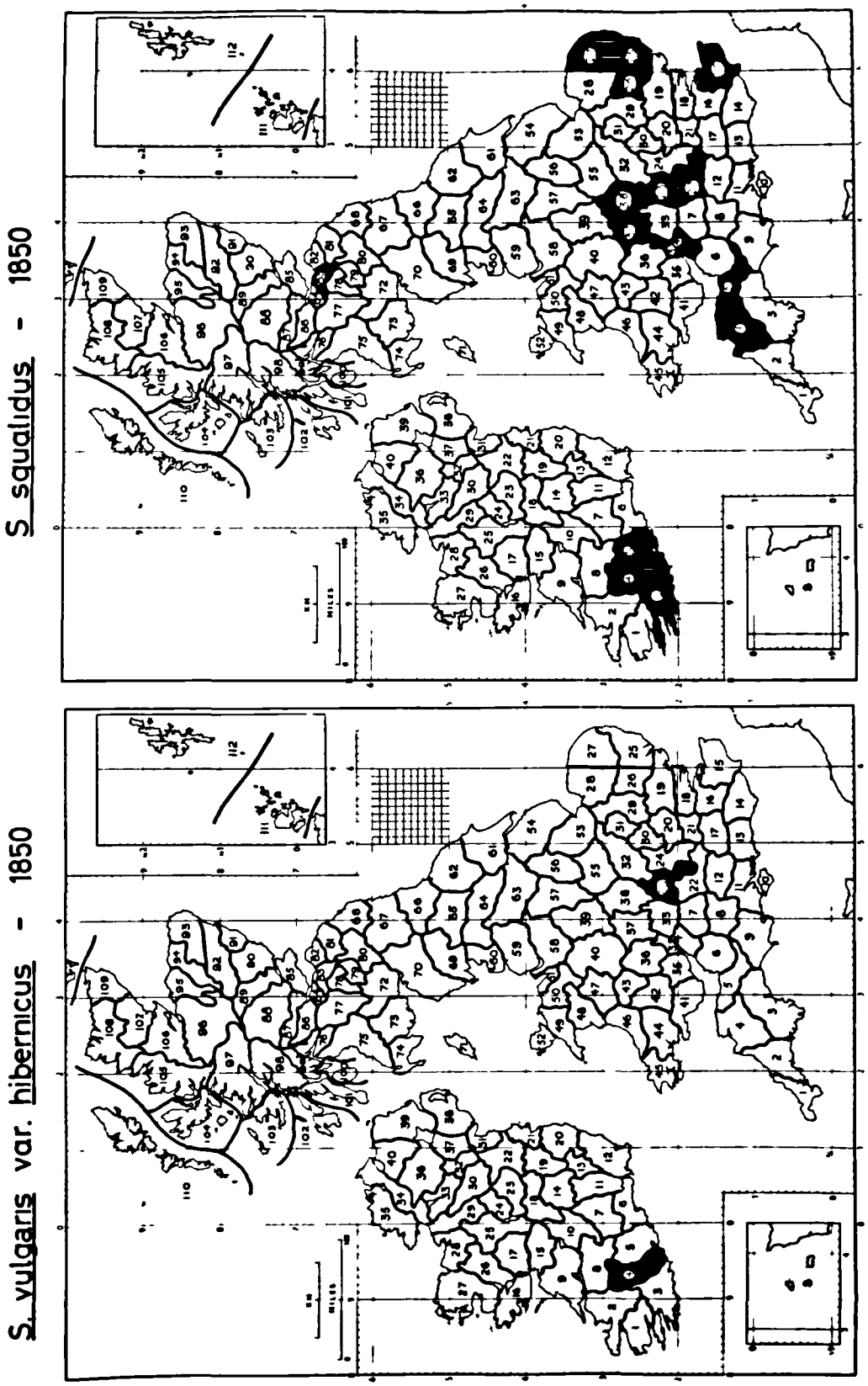
Most of the records of S. squalidus either duplicate, or refer directly to those of Kent (1955, 1956, 1957, 1960, 1964a, 1964b, 1964c, 1964d, and 1965) who has commented at length on the introduction and subsequent spread of this species in Britain. The spread of the species was affected by two main agencies besides the natural process of wind borne achenes. These were the great distributive potentials

Figure 12 The spread of Senecio vulgaris var. hibernicus and of S. squalidus

Data are presented on a Vice County basis: maps are the Botanical Society of the British Isles Vice County record maps (obtained from the Nature Conservancy Biological Records Centre).

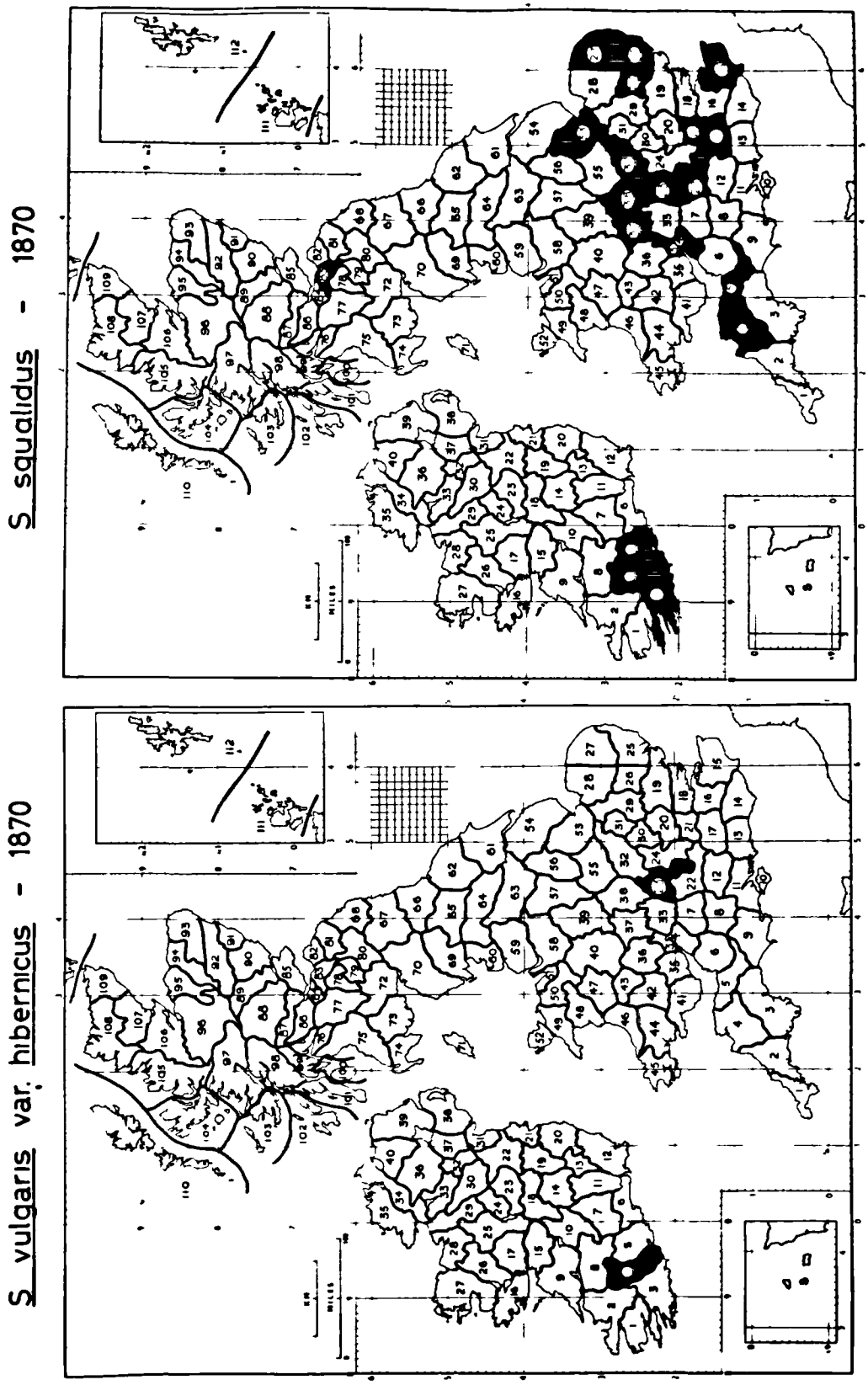
Data were drawn from herbaria and other sources given in Appendix Tables 11 and 12.





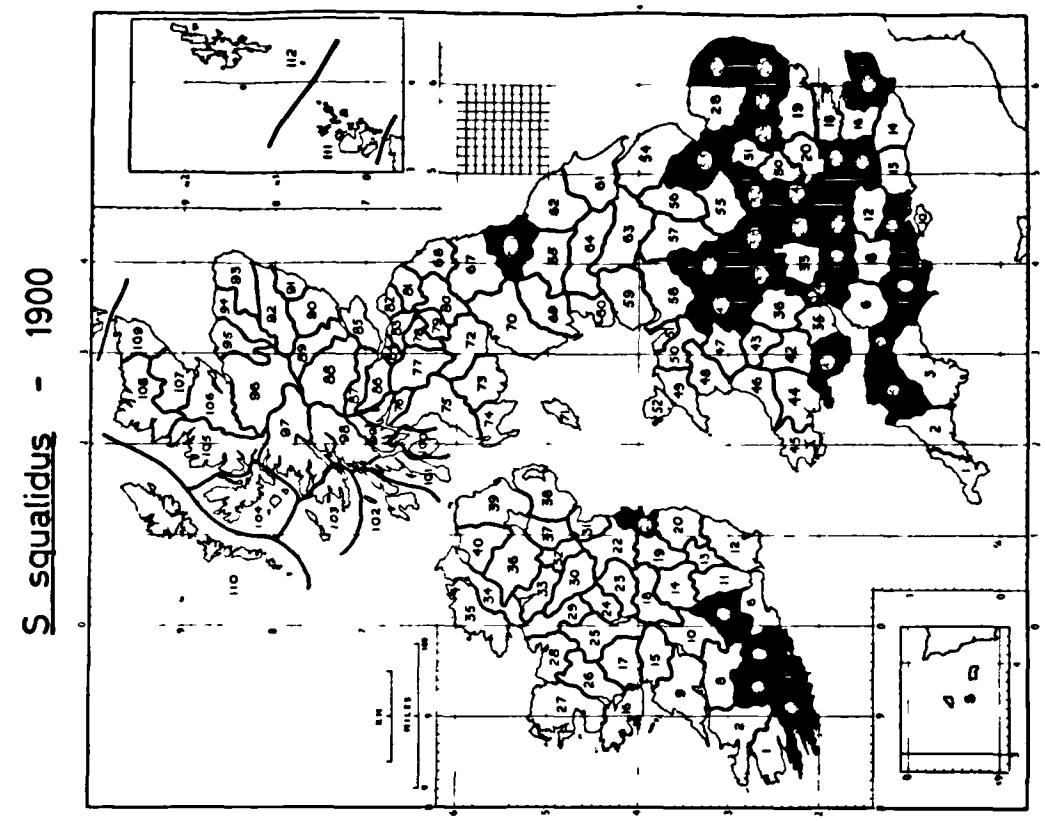
S. squalidus - 1850

S. vulgaris var. hibernicus - 1850

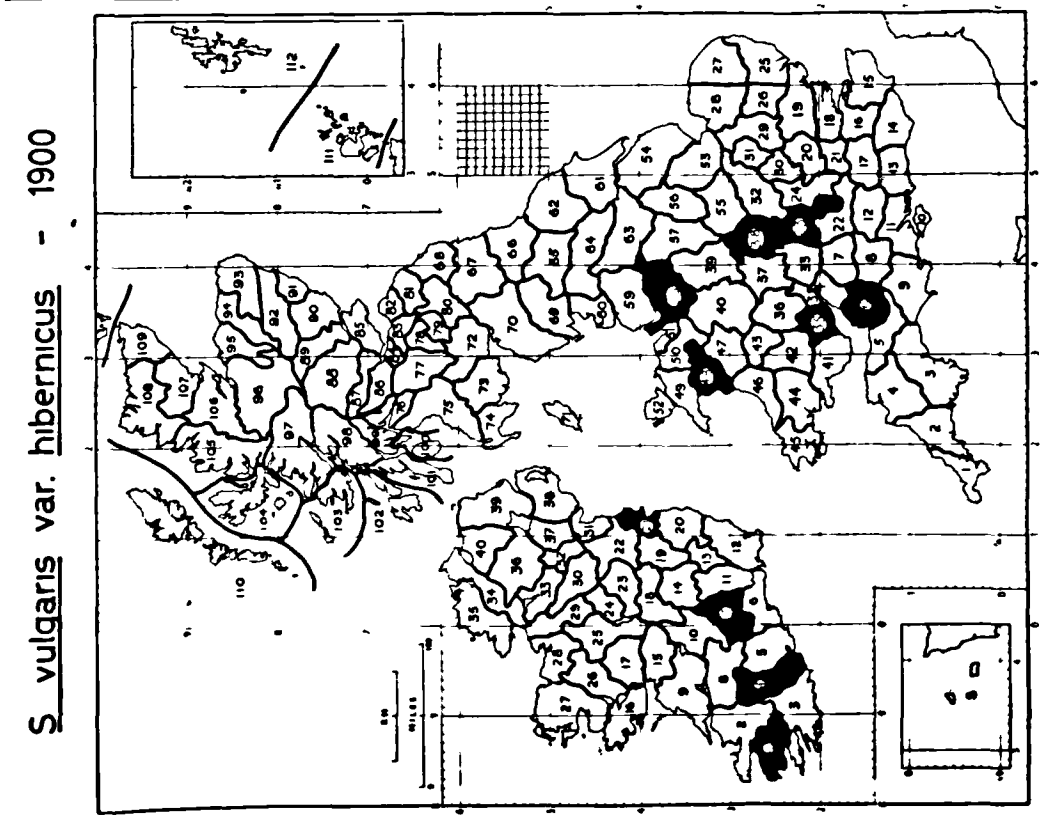


S squalidus - 1870

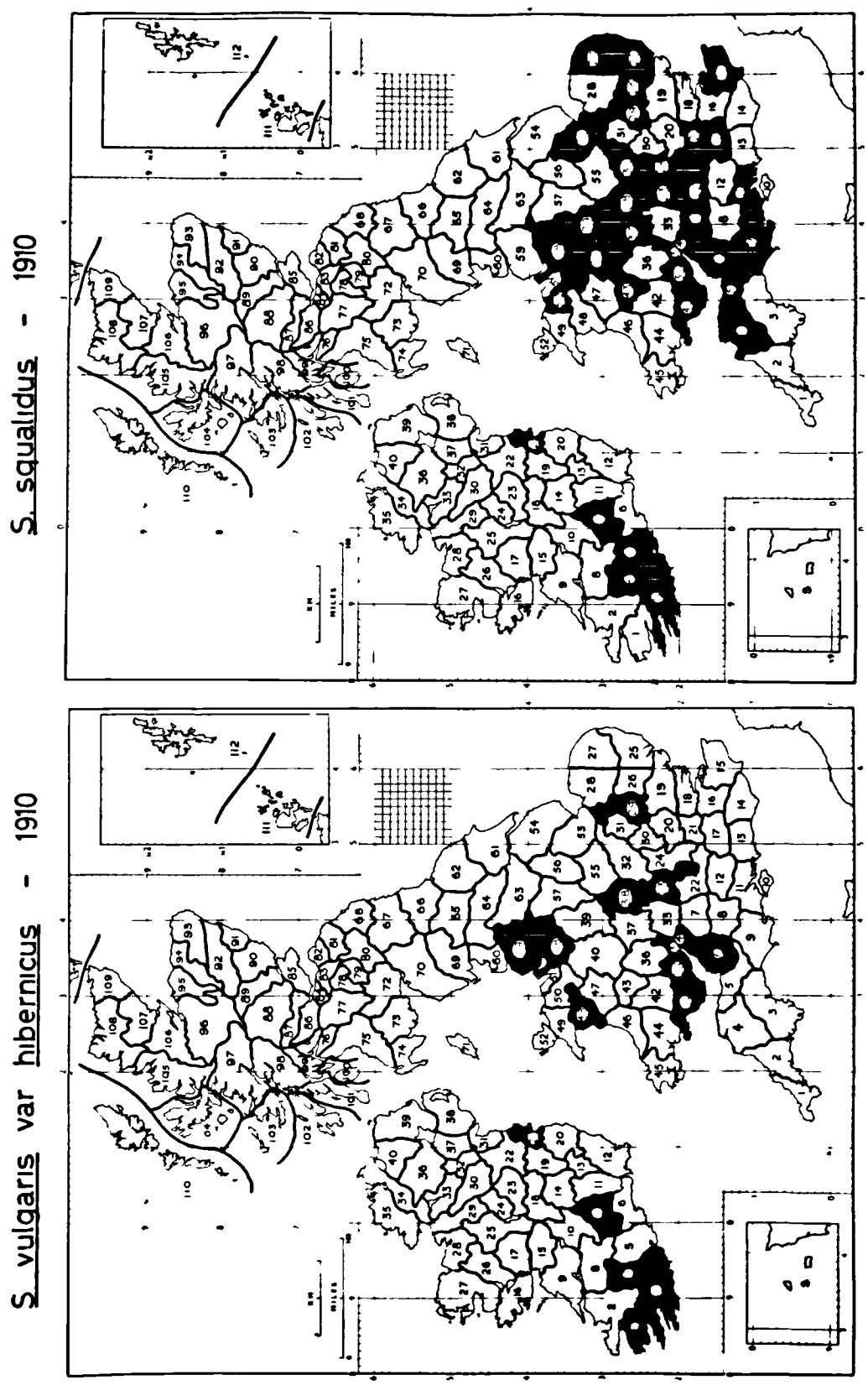
S vulgaris var. hibernicus - 1870



S squalidus - 1900

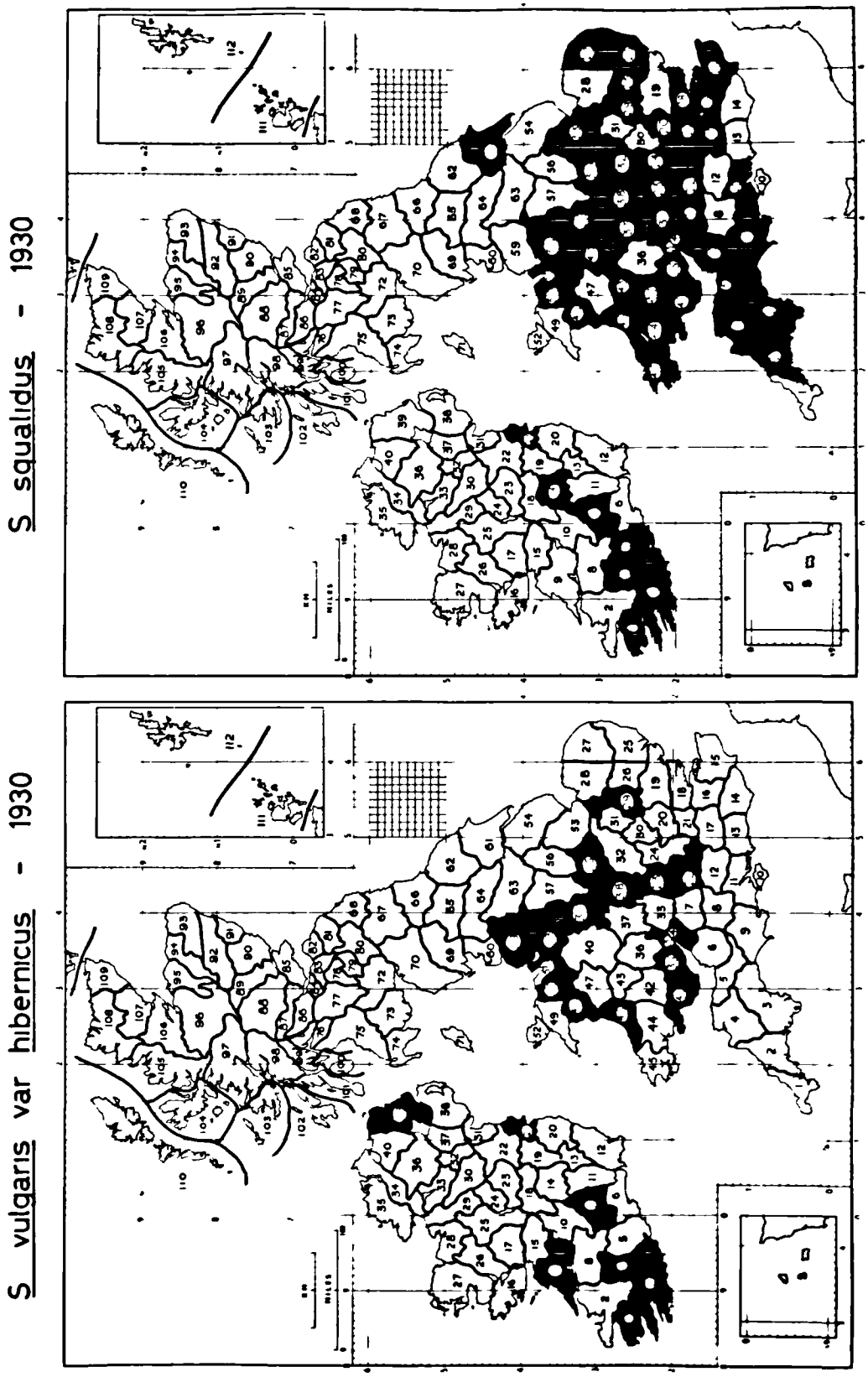


S vulgaris var. hibernicus - 1900



S. squalidus - 1910

S. vulgaris var hibernicus - 1910



S squalidus - 1930

S vulgaris var hibernicus - 1930

of railway vehicles - especially as the species grows well on railway shingles and cinders; and the transfer of material to different sites throughout the country by botanists. Comments to these effects have been included in the vice county record lists of the two taxa (Appendix Tables 11 and 12).

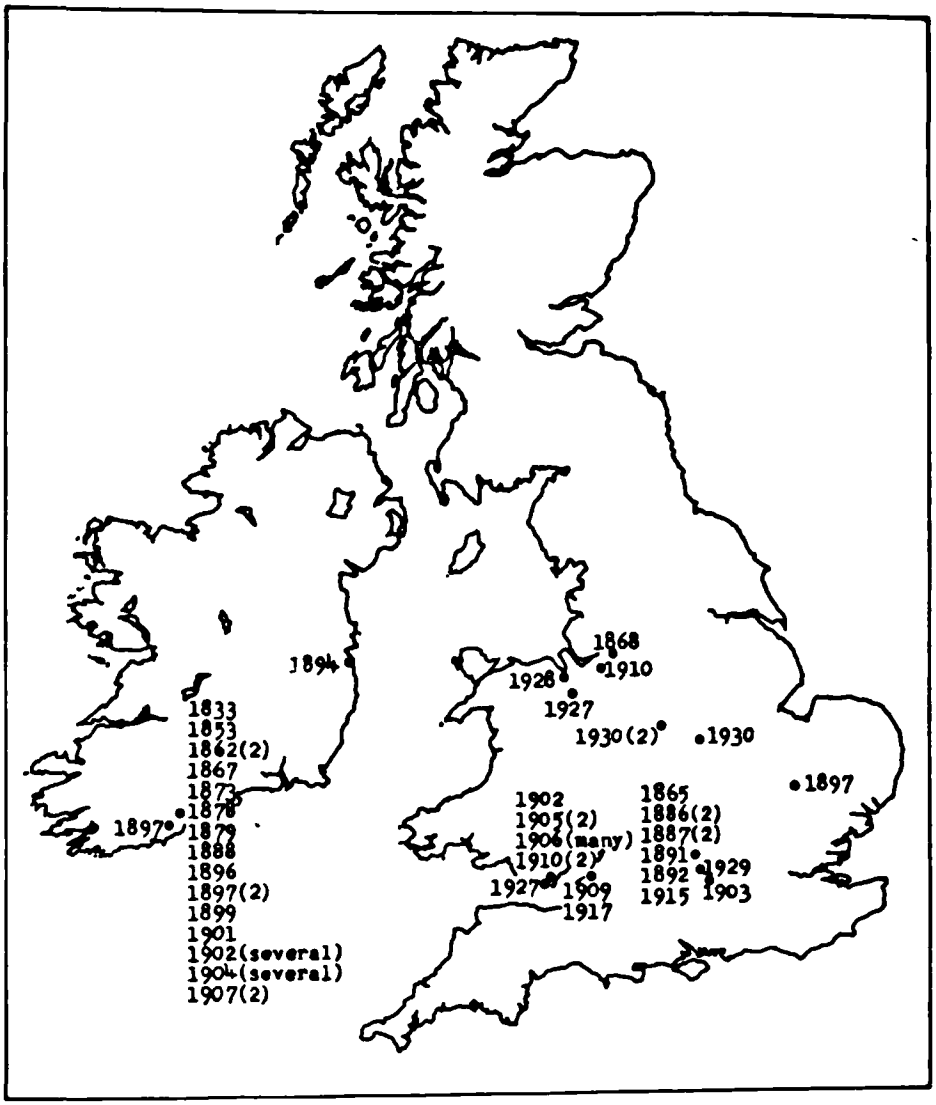
The series of maps given in Figure 21 shows the spread of the two taxa until 1930, when their common-ness and their ability to be distibuted independently over considerable distances had begun to blur the situation. The maps show clearly the tendency for var. hibernicus to appear only after S. squalidus had become established. Thus, var. hibernicus only appeared at Cork and Oxford following the establishment of S. squalidus outside of cultivation in these two places. Its subsequent appearance in Dublin coincided with the appearance there of S. squalidus. At about the same time, var. hibernicus arreared in the north Wales/Cheshire area, and around the Bristol Channel. Although in both areas it was collected before S. squalidus, it must be borne in mind that S. squalidus had become established prior to this in neighbouring areas.

Thus, up until about 1900 var. hibernicus had been recorded in four main areas: around Oxford; around Cork; the Bristol/Cardiff area; and the north Wales/Cheshire area. One must assume that introgression from S. squalidus (diploid) into S. vulgaris (tetraploid) cannot happen in a single step. If genes are transferred, they must pass via generations of one or more intermediate and backcross plants. Hence, the herbaria were searched for interspecific hybrids. This

search was greatly aided by observations of live material of this type (the S602 family which is discussed later), and the consequent characteristics looked for were: increased size and sterility of pollen and seed; anomalously shaped ligules; peculiar growth forms (indicative of unbalanced genetic control); and characters of an intermediate nature between the two species, such as ligule size, capitulum size, and leaf shape. In this way, plants of intermediate nature between S. squalidus and S. vulgaris were divided into three categories: those differing from S. vulgaris only by the possession of ligules - these were treated as var. hibernicus; those strictly intermediate, with complete pollen and seed sterility - these were assessed to be the sterile triploid F_1 (= S. X baxteri Druce), see Appendix Table 13; and those anomalous plants, not strictly intermediate, usually at least partially fertile, and possessing at least some of the characteristics of the S602 family. This last class was treated as being members of the early stages of the introgression sequence, and records of these are given in Appendix Table 14, and in Figure 12a. It must be pointed out, however, that it is very difficult to distinguish certain pressed specimens of this type from potentially hexaploid (equivalent to S. cambrensis) plants. Their pollen and seed size and fertility can be the same, and, as is described later, S. cambrensis is not uniform morphologically. Live specimens could, of course, be distinguished from S. cambrensis by the different chromosome number, and the different segregation

Figure 12a

Localities and dates, until 1930, of fertile intermediates between Senecio squalidus and S. vulgaris (based on inspected herbarium material):



Note: The Cambridge material (1897) was established in the Botanic Gardens from plants of Cork origin.

behaviour of their progeny (this is discussed in detail later).

Figure 12a shows that these anomalous specimens appeared around the localities where, up until 1900, S. vulgaris var. hibernicus had been recorded, rather than being correlated with the general spread of S. squalidus.

It appears probable, therefore that S. squalidus does form fertile intermediates with S. vulgaris, which lead to the introgression into the latter species of genes controlling expression of the ligulate character. From the historical evidence it is probably fair to assume that this introgression sequence takes place rarely, but in sufficient quantity to always result in the ligulate S. vulgaris appearing when S. squalidus is a common plant. The frequency with which the fertile intermediate plants have been recorded may reflect either the degree to which the introgression takes place, or that certain forms of these intermediates may persist for several generations. D.P. Young (personal communication) mentioned that progeny of a "giant rayed groundsel" collected in north Wales came true to parental type through several generations. It is quite possible, therefore, that the introgression sequence may be prolonged over an indefinite period, with the plants immediately capable of back-crossing into S. vulgaris being self maintaining.

INVESTIGATIONS OF LIVE MATERIAL INTERMEDIATE BETWEEN SENECIO VULGARIS AND S. SQUALIDUS

I have found only three cases in the field which I consider to be morphologically intermediate between S. vulgaris and S. squalidus, and distinct from S. cambrensis. Of these, extensive studies have been made only on the progeny of a plant found in November, 1966 on cultivated ground adjoining the Bromley-by-Bow gasworks in east London. This plant will be referred to as S602, and its progeny as the S602 family. The other two cases are discussed at the end of this Section (pp. 130-133).

Disturbed ground in London usually possesses extensive populations of S. squalidus, which often form the dominant ground cover over large tracts of ground. S602 was found on a moderately neglected allotment. S. squalidus was common both in the immediate and distant neighbourhoods of the plant, as was the ubiquitous S. vulgaris. To the untrained eye S602 only differed from S. squalidus in having ligules of about two thirds of the normal length. Observations of the plant when subsequently in cultivation revealed a number of additional characters (see Table 22), which, together with the short ligules, suggested that S602 was S. cambrensis, as described by Rosser (1955). Unfortunately further observations, including determination of chromosome number, could not be made on S602 before it died, and subsequent analysis was made on its autogamously produced progeny.

In all, about 100 of the immediate progeny of S602 were grown. They were remarkable because they exhibited a

Table 22

Comparison of Senecio squalidus, S. cambrensis, and S602:

character:	S. squalidus	S602	S. cambrensis
ligule length	means of 9.2 - 13.2 mm.	mean of 6.7 mm.	*0 - about 8 mm.
ligule number	13	13	*0, 8 - 13 (- 15)
middle cauline leaf shape (see Figure 13)	deeply or shallowly (bi-)pinnatifid; lobes parallel sided; auricles small, or occasionally absent	very similar to S. cambrensis, but less dissected	deeply and irregularly pinnatifid; lobes mostly parallel sided; auricles absent
pollen production	copious	copious	*limited in some races; fairly copious in others
pollen diameter	means of 22.1 - 27.4 μ	mean of 30.2 μ	means of *29.8 - 33.2 μ
pollen stainability	(91.2 -) 98.3 - 100.0%	83.4%	*65.1 - 96.1%
pollen pore number	3	3 and 4	3 and 4
achene length	means of 2.0 - 2.6 mm.	mean of 3.3 mm.	means of *2.4 - 3.5 mm.
achene set	0 - 100% depending on degree of pollination	68.2 %	*15 - 70%
breeding system	self incompatible and outbreeding	self compatible and inbreeding	*self compatible and inbreeding

Note: An asterisk (*) denotes that these characters of S. cambrensis are at least in part from my own observations; the others, which I have confirmed, are from those of Rosser (1955).

segregation of several characters, and that the somatic chromosome numbers of those studied were at about the tetraploid (2n = 40) level, - see Table 23. If S602 had been S. cambrensis, hexaploid progeny (2n = 60) would have been expected.

The segregating characters included several separating S. squalidus and S. vulgaris, and these are dealt with below.

Mildew (Erysiphe spp.) susceptibility was particularly noticable in several of the segregants, and was probably the direct cause of premature death in some of them. S. vulgaris, when grown in warm glasshouse conditions similar to those of the S602 progeny was found to nearly always suffer severe mildew attack, which could only be partially controlled by fungicidal application. S. squalidus occasionally showed slight mildew susceptibility, but in no case was this recorded as becoming severe.

The S602 segregants also showed a range of middle cauline leaf shapes and sizes (see Figure 13). In no cases did leaves appear which were indistinguishable from those of "typical" S. vulgaris or S. squalidus, and the closest resemblance was with those of S. cambrensis. Presumably, in this case, failure to segregate to either parental extreme reflects a complex genetic control of leaf shape. A lack of oligogenic effects has already been demonstrated in the range of leaf variation of the Sicilian S. squalidus taxa. It is of interest to note that S. vulgaris occasionally does appear with leaves of a similar type to those of S 602 (see Figure 13). In these cases the deeply dissected leaves and

Table 23

Chromosome numbers and ligule lengths of the autogamously produced progeny of S602:

mean ligule lengths (mm.):	0	1.5 | 2.5	4.6 | 9.5	10.8 | 11.0	12.2	TOTALS:
numbers of plants:	1	7	52	2	1	63
chromosome number (2n):						
36±1						1*
37						1*
38			1			1
39		1	1			2
40	1	3	21		1	26
41			1			1
42			1			1
						31(+2*)

An asterisk(*) indicates that the plant concerned died before flowering.

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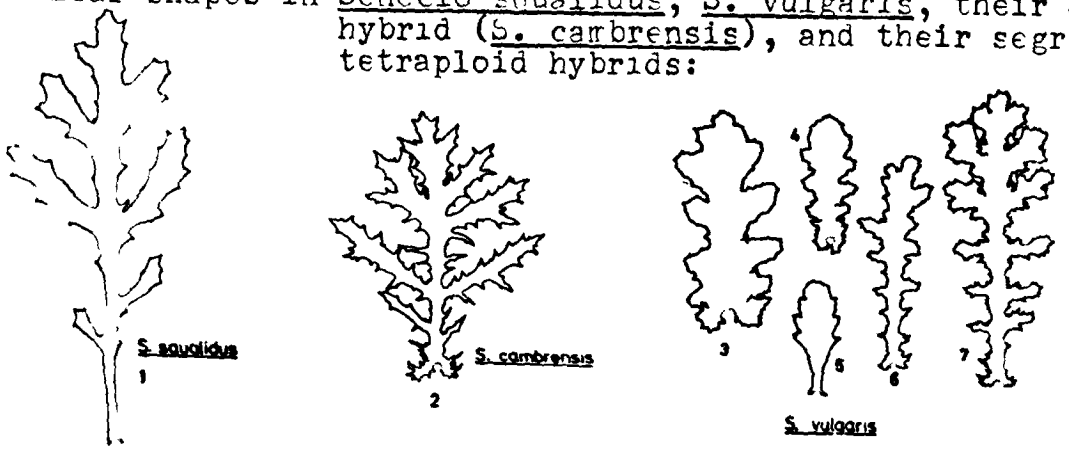
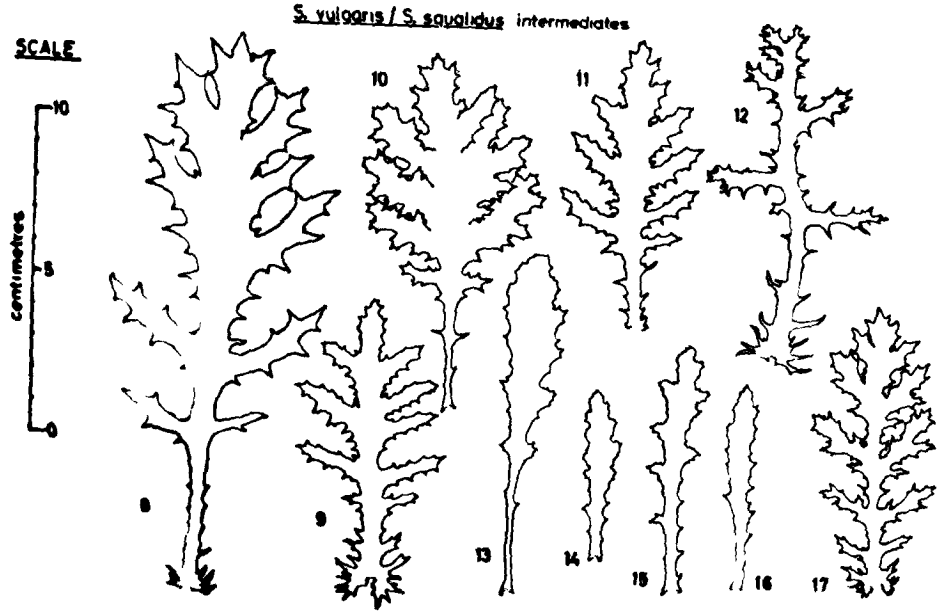
parallel sided lobes may possibly reflect the advent of introgressed genes from S. squalidus. I attempted to correlate this type of leaf dissection in S. vulgaris with the geographical spread of S. squalidus in Britain, as I have done for the ligulate S. vulgaris in the previous Section. Such a close correlation did not, however, become clear. Several herbarium specimens were found of S. vulgaris possessing this type of leaf before the appearance of S. squalidus in nearby areas. This indicates that this type of leaf is possibly an ancestral feature of the range of variation of S. vulgaris, although it might also be one of

Figure 13 Leaf shapes in Senecio squalidus, S. vulgaris, their allohexaploid hybrid (S. cambrensis), and their segregating tetraploid hybrids:





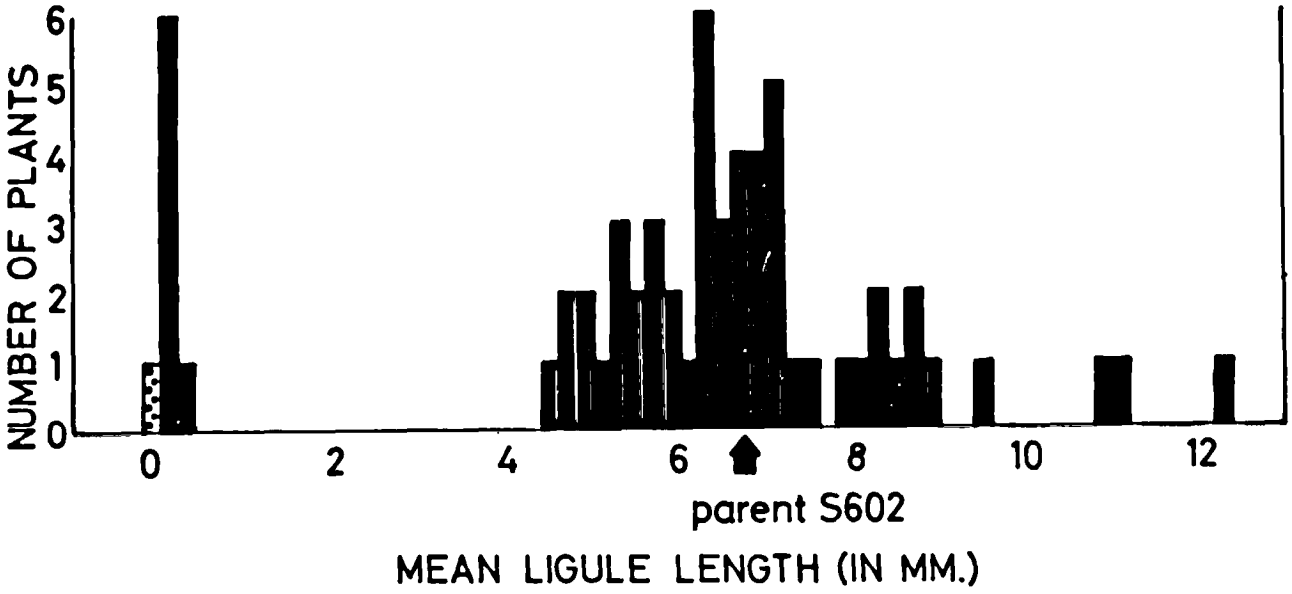
the products of recent introgression.

Ligule length was the most obvious segregating character in the S602 progeny (see Figure 14). Lengths form a discontinuous series from those of S. squalidus dimensions down to a complete absence of ligules, equivalent to the condition in S. vulgaris. There are no indications that variation in chromosome number involves chromosomes carrying these genes (see Table 23), and therefore the several classes of ligule lengths outlined below are probably a true reflection of different segregant genotypes.

S602 had a mean ligule length of 6.7 mm. (2 x S.E. of 0.20 mm.). Reference to Figure 14 shows that a minimum of five classes are apparent, consisting of one plant with no ligules; 7 with very small ligules (1.5 - 2.5 mm.); 52 with ligules of intermediate length (4.6 - 9.5 mm.); two with fairly long ligules (10.8 - 11.0 mm.); and one with a mean ligule length of 12.2 mm.. The last two classes are within the range of the British S. squalidus. Such a segregation, with the great majority of progeny around the parental mean, and with comparatively few individuals having segregated away from this mean indicates that several genes with similar effects are involved. It is probable that more than one class is incorporated in the 52 intermediates, thus possibly four classes can be made in this group: 4.6 - 6.0 mm. (17 plants); 6.1 - 7.5 mm. (26 plants); 7.9 - 8.8 mm. (8 plants); and 9.5 mm. (one plant). Thus it is possible that seven or more phenotypic classes are represented in the progeny of S602.

Figure 14

Length of ligules in the second generation of the S602 family:



Inheritance of the ligulate character in this family, as in S. vulgaris var. hibernicus, eligulate X ligulate S. squalidus, and in S. cambrensis appears to be additive in nature, with only partial dominance operative. Apart from this oligogenic effect, it is possible that the genetic background or the environment excerts a minor effect, as has already been suggested for var. hibernicus, and is indicated by the range of values in each of the classes of S602 progeny.

Only a limited analysis was possible of the second generation of the S602 progeny. The autogamously produced progeny of an S602 segregant (coded as S602:61) consisted of 6 plants with mean ligule lengths of between 4.4 and 5.3 mm. (corresponding to the previous generation's class of 4.6 - 6.0 mm.); and 9 with mean ligule lengths between 6.1 and 7.7 mm. (6.1 - 7.5 in the previous generation). None of these plants achieved the 8.6 mm. of its parent, despite growing conditions being very similar. This may have been due to segregation of a gene combination which displayed positive heterosis in S602:61, or it may, indeed, have been due to seasonal effects. The classes of ligule lengths in these plants support the classification given to the first generation.

When the autogamously produced offspring of the only eligulate S602 segregant (S602:32) were analysed, 16 were found to be eligulate, and one had very short ligules (mean length of 2.1 mm.). This indicates either that genetic suppressors of all or certain of the ligule promoting genes occur, or that more than one effective allele of the ligule promoting genes must be

present for expression of the ligulate character.

Because the chromosomal origin of S602 is not clearly understood, the genetic analysis of this situation is not possible.

Within the limits of the assumption that the same genetic system is operative throughout the S. squalidus/S. vulgaris complex, the following broad scheme can be postulated. The Sicilian S. squalidus shows a large range of ligule lengths, with no apparent oligogenic effects. This range must be the product of a polygenic system, the various intermediates being due to the additive effects of different combinations of alleles of the several genes involved. From this stock has evolved the British S. squalidus, which, in all but very rare cases, displays a relatively limited range of ligule lengths. This must be the result of a considerable increase in homozygosity for the genes controlling the character. S. vulgaris, which owes its phylogenetic origin to plants of similar constitution to S. squalidus is eligulate by virtue of mutations either of the ligule-promoting genes themselves, or of genes to render the ligule promoters ineffective. It is probable, therefore, that any ligule-suppressing gene (or genes) originated in S. vulgaris, rather than in the Sicilian or British S. squalidus. The lack of oligogenic effects in either of these two latter taxa supports this hypothesis.

The exception to the uniform ligule lengths in the British S. squalidus is the eligulate plant already referred to in the notes to Table 16 (see p. 73). Hybridisation between this

plant and a normal ligulate S. squalidus plant resulted in two classes of hybrids, both of intermediate ligule length. Of 19 of these plants grown, a 1:1 ratio of the classes was apparent, with 9 having ligules about 4 mm. long, and 10 having ligules about 7 mm. long. This may indicate that at least two genes were involved in a disomic system, one being heterozygous in each of the parents. The uniformity of populations for ligule length indicates that S. squalidus is probably homozygous at least for the majority of genes involved in the control of this character. Heterozygosity for the noticeable phenotypic effects was, therefore, probably in the eligulate plant. Possibly cryptic heterozygosity in the eligulate plant was due to heterozygosity of a ligule suppressing gene coupled with homozygous mutants of two ligule promoting genes. However, there is no other evidence to suggest that the ligule suppressing gene occurs in S. squalidus, and such a system necessitates the hypothesis that three genes have mutated and accumulated in a single genome. Alternatively, the same results can be obtained by postulating, as before, that more than one ligule promoting allele is necessary for expression of the character. In this case, of two ligule promoting genes in the eligulate plant, one would be heterozygous, the other mutant and homozygous. This alternative is more attractive because it suggests the accumulation of only two mutant genes.

The possible presence of ligule suppressor genes does not invalidate the hypothesis that the ligulate character is inherited by S. vulgaris as a single disomic gene, where one

must assume that all other relevant genes involved , including the suppressors, are homozygous.

The sex of the ligulate florets in the S602 progeny also segregated, and the degree of androecial development in these florets showed a very close correlation with the length of their ligules (see Table 24). A similar situation was noted in S. cambrensis, which is discussed in the Chapter on that species. This indicates that expression of ligule length and of androecial development are probably under at least the partial control of the same gene or linked genes.

It is interesting to note that such correlations do not apply to the Sicilian S. squalidus, or to the progeny of the ligulate X eligulate British S. squalidus, both of which always had full suppression of the androecium in ligulate florets.

This indicates that the increase in androecial development coupled with the decrease in ligule length has taken place in the ancestral S. vulgaris, possibly as an evolutionary response to the advent of inbreeding.

In the case of the eligulate S. squalidus plant, and in three investigated cases of eligulate capitula occuring on otherwise normal S. squalidus plants, the eligulate heads consisted solely of hermaphrodite florets. This shows that either no androecial development occurs in S. squalidus together with full ligule development within the limits of genetic determination, or full androecial development occurs together with no ligule development. Possibly this is due to an "all or nothing" hormonal effect, under wholly genetic control in

Table 24

Correlation of sex and ligule lengths in peripheral ligulate florets of segregants from S602:

segregant code no.:	state of androecial development:	mean ligule length (mm.):
S602:33	none	12.2
S602:40	"	10.9
S602:56	4 undeveloped filaments/floret	9.5
S602:42	4 " " "	8.8
S602:61	4 " " "	8.6
S602:53	2-3 " " "	8.6
S602:37	4 " " "	8.3
S602:60	4 " " "	8.0
S602:59	2-3 " " "	7.1
S602:51	4 " " "	7.1
S602:45	4 " " "	6.9
S602:28	4 " " "	6.9
S602:27	4-5 " " "	6.7
S602:48	4 partially developed anthers per floret; no pollen	6.3
S602:68	5 anthers with good pollen per floret; anthers smaller than those of disc florets	2.0
S602:32	5 fully developed anthers per floret; peripheral florets indistinguishable from disc florets	none

Note: 1. Ligule lengths are means of 10 measured from capitula with as near to 13 ligules as possible. In all cases 2 X standard error was less than 0.23 mm.

2. 10 - 20 peripheral florets were studied from a minimum of 3 different heads.

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the eligulate plant, and partially affected by the environment or by the endo-phenotype of the S. squalidus plants showing eligulate and ligulate heads. It is relevant to record that all three cases of eligulate heads on ligulate plants were found at the end of the growing season (October - November).

A number of other characters segregated in the progeny of

of S602. These were characters which could be associated with the hybridity *per se* of S602, rather than with the genetic differences of its parental species. Thus, many segregants showed increased fertility in the form of increases in pollen stainability and seed set (see Table 25):

Table 25 Seed set and pollen stainability in S602 and its autogamously produced first generation progeny:

		seed set %	pollen stainability %
S602		68.2	83.4
S602 progeny:	mean	42.4	76.9
	range	0.2 - 95.6	3.3 - 93.9

Note: Seed set in S602 was under isolated conditions. The figures for the S602 progeny are for conditions of open pollination, which, in those plants studied, were similar to those obtained under conditions only allowing self pollination. Seed set for the S602 progeny was determined from samples of 80 - 900 seeds from each of 26 plants; pollen stainability was determined from at least 400 grain samples from each of 19 plants.

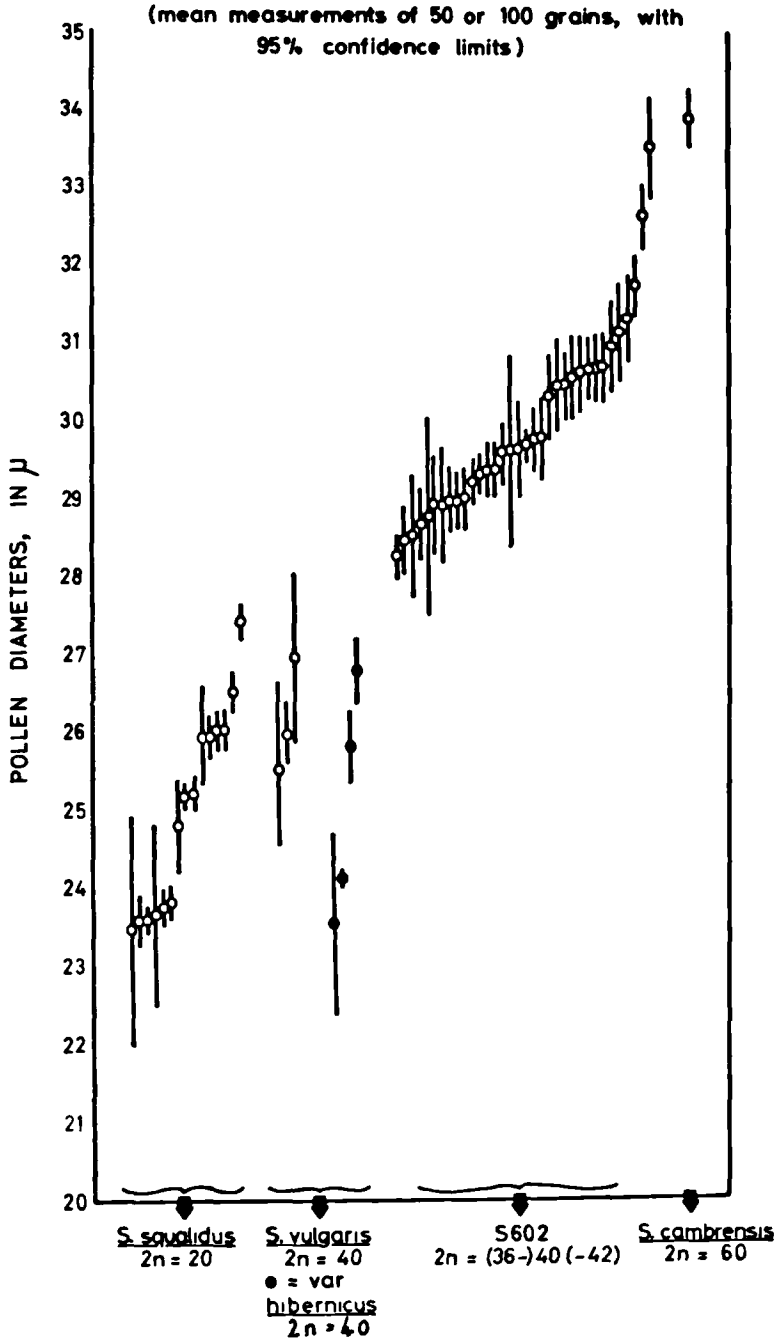
In addition, seed size tended to decrease: the parental S602 having a mean achene length of 2.9 mm., and its progeny ranging down from this size to the level of about the 2.5 mm. of the parental species (2.9 - 2.4 mm.).

Pollen size showed considerable variation in the S602 offspring (see Figure 15). In all cases the mean pollen diameter was greater than either of the parental species, and the largest were near to those of the natural allohexaploid *S. cambrensis* (measurements of *S. cambrensis* in the Figure are taken from Cambridge Botanic Garden material: other material

FIGURE 15

POLLEN DIAMETERS OF THE SENECIO SQUALIDUS / S. VULGARIS COMPLEX

(mean measurements of 50 or 100 grains, with 95% confidence limits)



of the species showed smaller pollen, see pp. 192). It is of interest that autotetraploid S. squalidus (see pp. 140-1) has pollen of similar dimensions to that of the largest of the S602 segregants. The following hypotheses can be made. The postulated origin of S. vulgaris from diploids similar to S. squalidus would originally have resulted in large pollen of the autotetraploid S. squalidus type. A fairly uniform optimum pollen size probably exists in Senecio, for several species (with the exception of hybrids and recent polyploids) investigated by me from different taxonomic positions in and close to the genus, and with different chromosome numbers (see footnote) have all proven to have pollen of similar sizes (i.e. ca. 24 - 29 μ). Pollen size is often taken in related taxa to indicate relative chromosome numbers, and hence relative chromosome mass. The fair uniformity of pollen size in Senecio must be the result of selection to either an optimum pollen size, or an optimum chromosome mass. The range of pollen sizes shown by the S602 segregants may be the result of disruption of of the balanced genetic systems controlling pollen size in the respective parent species. The alternative is that a reduction in chromosome mass followed the original tetraploidisation leading to the formation of the ancestral "S. vulgaris", without

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Footnote: Means of 20 or 50 pollen grains, in μ

	Kleinia articulata	2n = 20	29.0
Senecio section Jacobaeae	Senecio erucifolius	2n = 40	27.9
	S. jacobaea (3 plants)	2n = 40	27.7 - 29.0
	S. aquaticus	2n = 40	28.3
	S. linifolius (2 plants)	2n = 40	25.1 - 27.5
Senecio section Annui	S. aegyptius	2n = 40	27.3
	S. lividus (2 plants)	2n = 40	28.3 - 29.5

(other members of the Annui are elsewhere in the text)

a reduction in chromosome number. The range of pollen sizes in S602 and its family would, therefore, be the result of segregation of chromosomes and chromosome segments of unequal mass, probably exaggerated by unequal segregations due to meiotic irregularities. I made a few observations of chromosome masses in S. squalidus (2n = 20) and S. vulgaris (2n = 40) using Feulgen microdensitometry to measure DNA contents. The results were inconclusive and very variable, but indications were obtained that S. vulgaris may have possessed less than twice the DNA content of S. squalidus, even that the two species had about the same DNA contents. Unfortunately, the chromosomes of the two species were too small for me to follow up these observations by measurements of chromosome size to any degree of accuracy.

The number of pores in the pollen grain was also a segregant character. All species of Senecio investigated by me, as well as those mentioned in the literature (Faegri and Iversen, 1950; Batalla, 1940), besides their common size, had three pores per grain. Rosser (1955) reported the occurence of four as well as three pored pollen in S. cambrensis, - an observation supported by my own (see pp. 192). S602 and its segregants possessed various degrees of occurence of four pored pollen, ranging from being exclusively three pored, to virtually all being four pored (see Table 26). Four pored grains also occur in the auto--tetraploid S. squalidus. They were also common in the S. squalidus/S. viscosus families discussed in the Chapter on S. X londinensis. Four pored grains, therefore, appear to occur commonly in taxa of hybrid or polyploid origin. These taxa also

Table 26

The occurrence of supernumerary pores in pollen of the S602 family, and the lack of correlation of this with pollen stainability or size:

Table 26a In first generation progeny of S602:

plant	pore number	mean size in μ	standard deviation in μ	% stained
S602:1	all 3 pored	27.7	1.2	74.2
S602:13		28.8	2.1	86.5
S602:14		29.2	1.8	73.6
S602:16		29.3	1.5	45.7
S602:10		29.9	1.4	90.1
S602:20		30.1	1.4	80.6
S602:7		30.1	1.9	74.8
S602:3		30.8	2.2	73.9
S602:8		30.9	2.0	56.9
S602:12		31.0	1.8	68.3
S602:17		31.3	1.9	67.5
S602:4		31.5	2.1	74.8
S602:19		31.7	2.2	92.2
S602:15	very few 4 pored	29.3	1.7	67.4
S602:6		29.3	1.9	81.5
S602:18		31.1	1.5	78.6
S602:2	some 4 pored	28.8	2.6	67.9
S602:9		29.0	1.6	47.1
S602:5	mostly 4 pored	30.0	1.4	87.5

Table 26b In progeny from a single S_1 from S602:

plant	% with each pore number				mean size in μ	s. d. in μ	% stained
	3	4	5	6			
S602:61:16	98	1	1	0	29.7	1.3	85.2
S602:61:10	96	4	0	0	30.2	1.3	87.8
S602:61:9	92	2	4	2	29.7	0.9	90.4
S602:61:7	58	30	10	2	28.4	1.3	77.3
S602:61:8	56	44	0	0	29.7	1.2	84.4
S602:61:15	56	34	6	4	28.2	1.7	78.5
S602:61:13	22	74	2	2	29.8	1.4	88.4
S602:61:17	22	68	6	4	29.6	1.0	89.8

Note: Samples for size and pore number were of 50 or 100 grains; samples for stainability were at least of 400 grains.

share the phenomena of variability in pollen size, large mean pollen size, a degree of pollen sterility, and pollen mother cell meiotic irregularities. The occurence of four pored pollen could not, however, be correlated with any of these other phenomena in the S602 family, although no measure could be made of the degree of meiotic abnormalities (see Table 26). The occurence of variable numbers of pores was also noted in the Sicilian S. squalidus (see pp. 60-63), but this appears to be of a different type, and may be the result of different controls. Similar increases in pore numbers associated with polyploidy have been noted in other species. Thus Funke (1956) reported polymerous pollen grains in Brassica juncea, B. carinata, and natural polyploid Solanum species compared with their respective diploid ancestors. Reese (1956) noted four pored grains in autotetraploid progeny of the normally trimerous diploid Aster capensis. Najčevska and Speckmann (1968) observed similar relationships between diploid and tetraploid varieties of three species of Trifolium. The last authors also failed to find a correlation between pore number and pollen size.

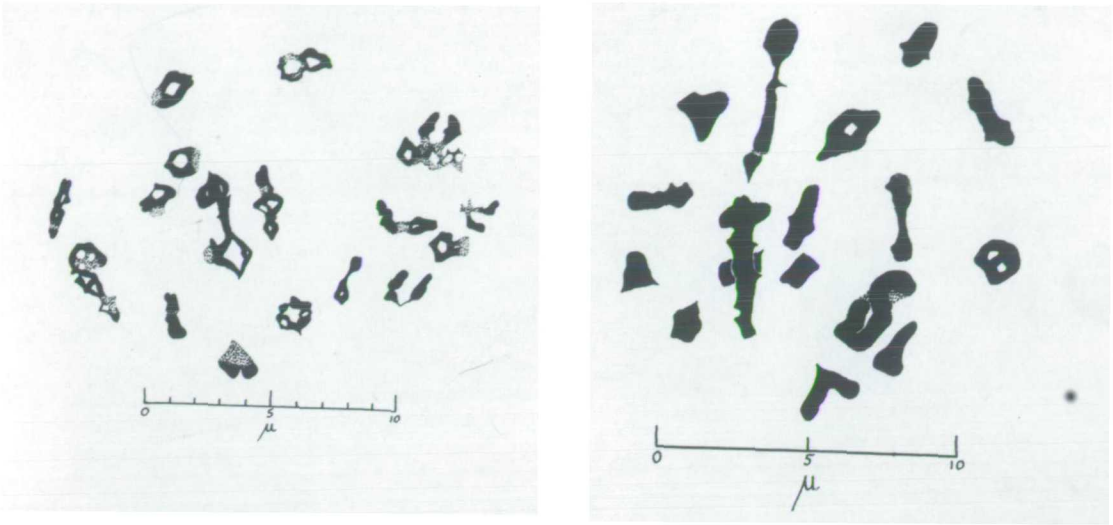
No segregation was noted in the S602 family of the self-incompatibility/self-compatibility systems. All proved to be self-compatible, and no increase in seed set was noted when in conditions of open pollination.

S. vulgaris is monocarpic, whereas S. squalidus is polycarpic. All of the S602 first generation progeny were polycarpic. Possible exceptions were several of the progenies of the eligulate S602:32, which became diseased, and died shortly

after flowering. It was not clear whether death was an inherent physiological feature, or a consequence of general debility. However, such a course of events is common in the monocarpic species, and this may have been another segregating character in the S602 family.

The main point of interest in this second generation from S602 was the close similarity between S. vulgaris and several of the offspring of the eligulate S602:32. Apart from the greater size of these plants, a detailed examination was necessary in order to separate these plants from S. vulgaris. The plants had slightly larger pollen grains and seeds than S. vulgaris normally does, but neither of these features could be considered as being outside of the normal range of the species. Similarly, both pollen stainability and seed set were slightly lower than is normally met with in S. vulgaris. The leaf type was indistinguishable from that often seen in S. vulgaris (see No.7, Figure 13, p.114). The tendency towards polycarpy, already mentioned, was the most noticeable difference from S. vulgaris. In all cases where the somatic chromosome number was determined (10 of the 17 plants grown), it was found to be the normal tetraploid number of 2n = 40, as was the parent S602:32. Pollen mother cell meiosis usually appeared to be regular, although occasionally a small amount of chromosome material would be seen lagging or excluded from telophase nuclei. In several cases a fairly low incidence of multivalent formation could be discerned, and drawings are given (see Figure 16) of two of these metaphase plates, where three quadrivalents and 14

Figure 16 Camera lucida drawings of metaphase plates from pollen mother cells of progeny of the eligulate S602:32 (a tetraploid of hybrid origin between Senecio vulgaris and S. squalidus):



bivalents could be clearly seen. Meiosis in S. vulgaris has always been found by me to consist of 20 bivalents in plants investigated (see Table 8, p. 33).

Another progeny of S602, S602:49, was used to pollinate an emasculated, eligulate S. vulgaris plant. S602:49 was ligulate, and it was hoped that hybrids could be detected by using the ligulate character as a marker. Unfortunately, a degree of selfing and a very low seed set did not allow any genetical analysis to be made as a result of this hybridisation and only three plants of probable hybrid origin were obtained. These plants were fairly heavily infected with mildew (as were the self-produced progeny of S602:49), and this may have reduced their development, as well as not allowing an estimation to be made of their proper degree of monocarpy. All three plants were of the same order of size as might have been expected in

S. vulgaris, and died shortly after flowering. Leaf shape closely resembled that of the S602:32 progeny and as such was within the range of variation of S. vulgaris. Pollen stain-ability was in every case over 95%, but seed sets were respectively 59%, 62%, and 73%. A reduced seed set is quite common in mildew infected Senecio plants, and these seed set results may have potentially been as high as the 95 - 100% of S. vulgaris. Mean pollen and seed sizes were reduced from S602:49 mean sizes of respectively 28.2 μ and 2.8 mm. to 25.8 - 27.2 μ and 2.4 - 2.6 mm., which are both within the range of variation of S. vulgaris. The plants only differed from S. vulgaris in their ligule development. The ligules, although shorter than in S602:49 (mean lengths were 2.2 mm., 2.3 mm., and 4.8 mm. as opposed to the parental 6.5 mm.), were broader than than those usually found in var. hibernicus (means of 2.3 mm., 2.3 mm., and 2.4 mm., respectively) which usually has ligules of 2.0 mm. or less in breadth. The shorter (2.3 and 2.2 mm.) ligules also had a more marked dissection of their tips into the component petals than is found in the ligules of equivalent length in the ligulate X eligulate S. vulgaris heterozygotes.

To summarise, these plants descended from putative hybrids between S. vulgaris and S. squalidus only differed recognisably from S. vulgaris by the form of their ligules. It has already been shown that a number of genes are involved in the expression of the ligulate character. Although this single backcross from S602 into S. vulgaris has failed to provide hibernicus-type

ligules, it is possible that further backcrossing and segregation would have resulted in the single gene difference separating var. hibernicus from var. vulgaris. Presumably only one of the several genes involved in ligule determination ends up in the bi-allelic condition in S. vulgaris, for despite the probability that var. hibernicus has arisen on a number of separate occasions, the form of its ligule is fairly constant. This may be the result of selection, and the lack of any obvious selective advantage in the ligulate condition might indicate that the internal balance of the S. vulgaris genome is not upset by the alternative allelic form of this one gene. Selection favouring the other genes involved in ligule expression must have have resulted in the normal vulgaris genes being retained in the homozygous condition.

An exception to this type of ligule in var. hibernicus was a single plant, found by me in June, 1967 on a roadside in Newbridge-on-Wye, Radnorshire. The plant was typical in every respect of var. hibernicus, except that its ligules had a mean length of 8.1 mm., and a mean breadth of 3.2 mm. (as opposed to usual maxima of, respectively, 6.0 mm. and 2.0 mm. in var. hibernicus). Self produced progeny were grown from this plant through two generations, and of the 10 plants involved in each generation, no segregation of ligule characters away from the parental type was noted. This population may have become fixed with more than one ligule promoting genes. The possible significance of the persistence through consecutive generations of the intermediates in the introgression sequence is discussed

6n pp.134-135.

The third example of this type of plant found by me in the field was in a large number of S. vulgaris plants growing in the Genetics Gardens of the Birmingham (Edgbaston) University in October, 1969. In addition to the many normal eligulate S. vulgaris plants present, about 50 atypical plants were found. These were typified by possessing capitula of S. squalidus dimensions, which formed a marked contrast with the neighbouring S. vulgaris. They had leaves of the well dissected S602:32 type previously described, and were generally rather larger and thicker stemmed than S. vulgaris. About 40 of these plants had ligules about 6 mm. in length, and about 3 mm. in breadth, that is, noticably wider than in var. hibernicus. Two plants had short, wide ligules (about 2.0 mm. X 2.5 mm.), and the rest were eligulate. Achenes were 3.0 - 3.5 mm. in length (as opposed to about 2.5 mm. in the neighbouring S. vulgaris). Rapid observations of pollen size showed it to be appreciably larger than that from the neighbouring S. vulgaris. Seed set and pollen stainability were both high, accurate counts were not made, but I estimated them to be greater than 80%. Inquiries in both Departments of Botany and Genetics in the University revealed that Senecio material had not been used for research or teaching.

One plant in the Birmingham population was particularly noteworthy. This was completely seed sterile, and the florets and pappi had elongated to about one and a half times their normal lengths. The receptacles followed the normal procedure

associated with seed release, and formed a convex surface, but no loss of florets ensued, with the consequence that many very distinctive "pom-pom" heads were present on the plant. It is of interest to note that a similar plant is in the Kew Herbarium, gathered from Cardiff in 1928 (by W. Nelmes). It is more likely that the plant in the Birmingham population is the product of a particular aberrant genetic combination, rather than the chance product of a mutation. Possibly the Cardiff plant owns a similar origin, and indicates that a similar population of S. vulgaris X S. squalidus existed nearby.

No chromosome counts were made of plants from this population, and so the equal possibilities exist that these plants were hexaploid (equivalent to S. cambrensis) or tetraploid (equivalent to S602). However, the segregation shown by this population indicates a higher likelihood of them being of the S602 type, although no data is available of the segregational behaviour of the newly formed S. cambrensis.

SUMMARY

Several of the characters of the S602 family, such as increased pollen and achene sizes, and the leaf shapes, were unexpected in the S. vulgaris/S. squalidus intermediates. As such, the observations made on the S602 family proved invaluable when herbarium specimens were assessed. A great deal more certainty could be attached to identification of anomalous specimens, the product being Figure 12a(p.108), which indicates herbarium specimens identified by me as probably being of the S602 type. The possibility does, however, exist that several

of these plants are of the S. cambrensis rather than the S602 type, and I know of no way by which certain segregates of the S602 type can be distinguished from S. cambrensis without a count being made of the chromosomes.

It is now possible to outline a possible scheme for part of the sequence of introgression of genetic material from S. squalidus into S. vulgaris. From the point where S602 type families have become established, the inter-related processes of segregation and back-crossing into S. vulgaris must proceed with the eventual formation of gene-enriched S. vulgaris populations. Several phenomena will probably be associated with this sequence. The very varied, and in some cases, unbalanced genetic types segregating out must be subject to selection (such as against "pom-pom" and mildew susceptible types). Selection will also favour fertility, and thus, presumably, a balanced meiosis based on the tetraploid chromosome number. Selection will therefore be towards the normal balanced tetraploid chromosome complement of S. vulgaris. One might therefore expect the repeated segregations (assoc--iated with inbreeding) to tend towards the S. vulgaris genotype, this process being accelerated by new influxes of S. vulgaris genes by back-crossing. Occasionally recognisable intermediates in the introgression sequence may persist through several generations. Examples of this latter phenomenon may be the large-liguled var. hibernicus from Newbridge-on-Wye, the odd segregational behaviour shown by the Brymbo strain of var. hibernicus, and the series of S602-like plants (which are well represented in the herbaria, see Appendix pp. 283-7)

found in the Cardiff Dock area between 1902 and 1910.

Two important points can now be made. One is that an initial hybridisation between S. vulgaris and S. squalidus may lead to the establishment of a population of intermediates which are responsible for repeated influxes of S. squalidus genes into the S. vulgaris gene pool, and as such act as a long term reservoir of genetic variability for the latter species. This also means that the original hybridisation between the two species need only be a very rare event, and yet can be responsible for considerable gene flow. The second point is that the ligulate character is, in itself, possibly of no selective importance to S. vulgaris, and introgression may proceed without the ligule character being involved, - as is shown in the products of the eligulate S602:32. In other words, the ligulate character of var. hibernicus is probably only a marker that introgression has taken place, the true evolutionary importance of the introgression lying with other, less easily identified genetic controls (a possible example is mildew resistance).

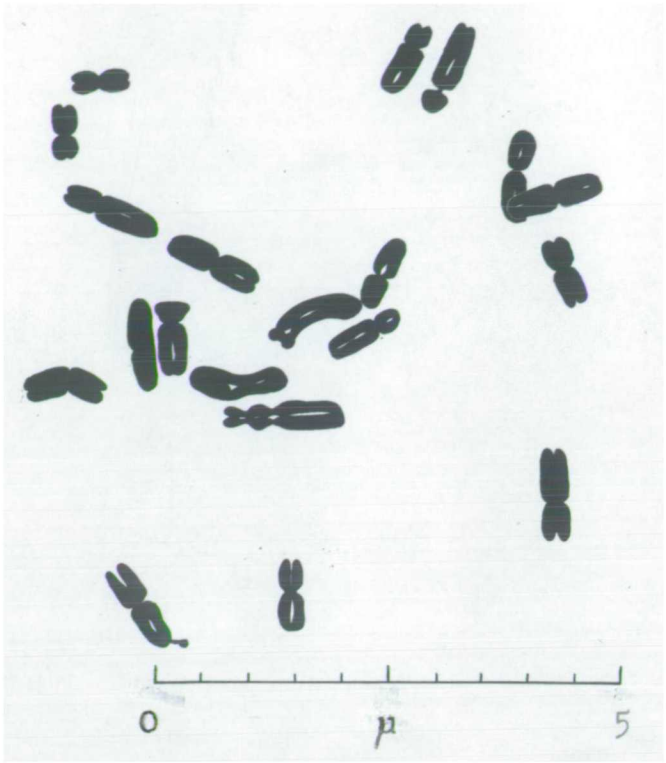
THE POSSIBLE MECHANISMS FOR INTROGRESSION FROM SENECIO SQUALIDUS INTO S. VULGARIS

The precise method, or methods, by which the initial stages in the sequence of introgression from S. squalidus into S.vulgaris has not been definitely determined. The possibility exists that S602 was an F_1 hybrid formed directly by the combination of an unreduced S. squalidus gamete (2n = 20) and a reduced S. vulgaris gamete (n = 20), but several alternative and less direct origins are also possible. No other evidence has been found in the field which throws light on the initial stages of introgression. Therefore, the mechanism must be postulated on the basis of experimental evidence. There are four possibilities for the origin of plants of the S602 type - that is, of segregating tetraploids of hybrid origin - and these will be dealt with in turn.

1. INTROGRESSION VIA AUTOTETRAPLOIDY OF S. SQUALIDUS

S. squalidus, in all instances in which I have observed it (see Table 27) has been diploid, with 2n = 20 (see Figure 17). Presumably diploids similar to S. squalidus were phylogenetically ancestral to the monocarpic tetraploid group, including S. vulgaris, and it is possible that the doubling of chromosome number was associated with, and may have been directly responsible for evolutionary change. However, it is also possible that the process of tetraploidisation per se may have recognisable morphological effects. The gigas effect of polyploidisation is the most frequently quoted, but other characters, such as

Figure 17 Camera lucida drawing of the chromosomes of Senecio squalidus from a root tip cell:



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hormonal balances, may also be effected (Noggle, 1946), and could result in unexpected changes. It is conceivable that the sex of Senecio florets is under hormonal control, and, as has already been shown in the S602 family, there may be a negative correlation between expression of male-ness and the ligulate character. Samata (1964) suggested that ligules and disc floret anthers in Compositae are mutually exclusive becaues of early competition for metabolites, but Rana (1965) showed that the characters are genetically separable in Chrysanthemum carinatum. Hormonal applications have been shown to effect the sex ratio of flowers in monoecious Cucurbit plants (Laibach and Kribben, 1951; Laibach, 1951). More

Table 27 Chromosome counts in *Senecio squalidus*:

source	2n =	n =	comments
SICILIAN MATERIAL			
Mt. Etna, Sicily	20	10	counts from 12 plants derived from 7 Etnan populations of *S. aetnensis*
		10	counts from 8 plants derived from 3 Etnan populations of *S. X incisus*
Mt. Etna and Catania, Sicily	20	10	counts from 10 plants derived from 4 Sicilian populations of *S. chrysanthemifolius*
BRITISH MATERIAL			
Staines, Middlesex		10	counts from 3 plants
Longcross, Surrey	20	10	counts from 10 derivatives of 2 Longcross plants
Egham, Surrey		10	counts from 2 plants
Watford, Herts.		10	counts from 2 plants
Mile End and Stepney, London E.1		10	counts from 12 plants from 3 populations
Stratford, London E.3		10	counts from 3 plants
Manor Park, London E.12		10	count from 1 plant
Poplar, London E.14	20	10	counts from 1 plant
Oxford	20	10	counts from 15 plants from 5 populations
Didcot, Berks.		10	counts from 2 plants
Reading, Berks.		10	counts from 4 plants
		9	count from 1 seed-sterile plant
Moss Side, Manchester		10	count from 1 plant
Wrexham, Denbigh.	20		counts from 4 plants
Ffrith, Flintshire	20	10	counts from 6 plants
Chester, Cheshire		10	counts from 2 plants
BOTANIC GARDEN MATERIAL			
Hort. Bot. Bergianus, Stockholm, Sweden	20	10	counts from 4 plants
Hort. Bot. Universitatis, Uppsala, Sweden		10	counts from 3 plants
Mus. d'Hist. Nat., Paris, France		10	count from 1 plant
EXPERIMENTAL MATERIAL			
Dr. K. Goodway, Keele University, Staffs.	20	10	an eligulate plant, discussed in text

- continued -

derivatives by open pollination of material from Hort. Bot. Bergianus, Stockholm, Sweden	40	20	CS2	colchicine induced C_0 autotetraploids
	40		CS3	
		20	CS8	
	40		CS10	
	40		CS11	
	40	20	CS12	
	40		CS13	
		20	CS16	

recently, Rana and Jain (1968) induced re-expression of the male character in the ligulate florets of a mutant male-less Cosmos bipinnatus by gibberellin application. They suggested that the expression of the mutant male-less character, both with and without gibberellin application, was also dependent on genetic background (Rana, Jain and Nerwal, 1963; Rana and Jain, 1968). Probably controls of the ligulate character and male expression operate at several levels between the genotype and the phenotype, and I considered it necessary to investigate the effects of autotetraploidy on Senecio squalidus.

Autotetraploids were produced of a range of S. squalidus by colchicine treatment of young seedlings or axillary buds. Selection of plants on which the treatment might have been successful was based on damage and malformities at a young stage (leaves and stem thick and mis-shapen), and a slower growth rate than the untreated or unaffected plants or parts of plants. After the initial stages of growth following colchicine treatment, no morphological differences were discernable in plants successfully rendered tetraploid, until flowering could be observed. Flower dimensions in these somatic tetraploids (termed generation C_0) were similar to the diploids and could

Table 28 Numbers of apertures and diameters of stainable pollen of diploid and autotetraploid Senecio squalidus:

	diploid	tetraploid
pollen diameter		
small (23 - 30μ):	99.8 - 100.0%	0.0%
large (31 - 37μ):	0.0 - 0.2%	100.0%
number of apertures		
small pollen	3	-
large pollen	3 or 4	3 or 4

These data are derived from British Senecio squalidus, including 15 diploid, and 6 C_0 and 12 C_1 autotetraploid individuals.

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not be used as a criterion of tetraploidy. Only in their larger and less fertile pollen (Table 28 and Plate 5) and seed (Table 29) could the C_0 tetraploids be distinguished from the diploids without observing chromosome numbers in their pollen mother cells or in root tips from established cuttings. Progeny from these C_0 tetraploids (that is, the C_1 generation), however, displayed gigas characters, which will be discussed later. Table 30 gives details of chromosome behaviour in the pollen mother cells of the C_0 autotetraploids, which was of a fairly regular nature.

The most interesting of the differences between the diploids and the C_0 tetraploids was that the latter were self-fertile. Isolated plants, and bagged heads of these C_0 tetraploids set up to about 20% good seed. Under conditions of open pollination seed set was often higher (up to about 30%), but no analysis was made of these observations.

Self incompatibility mechanisms in plants have been subject to considerable investigation in recent years, and are broadly

Plate 5A & B Pollen of diploid and tetraploid Senecio squalidus:

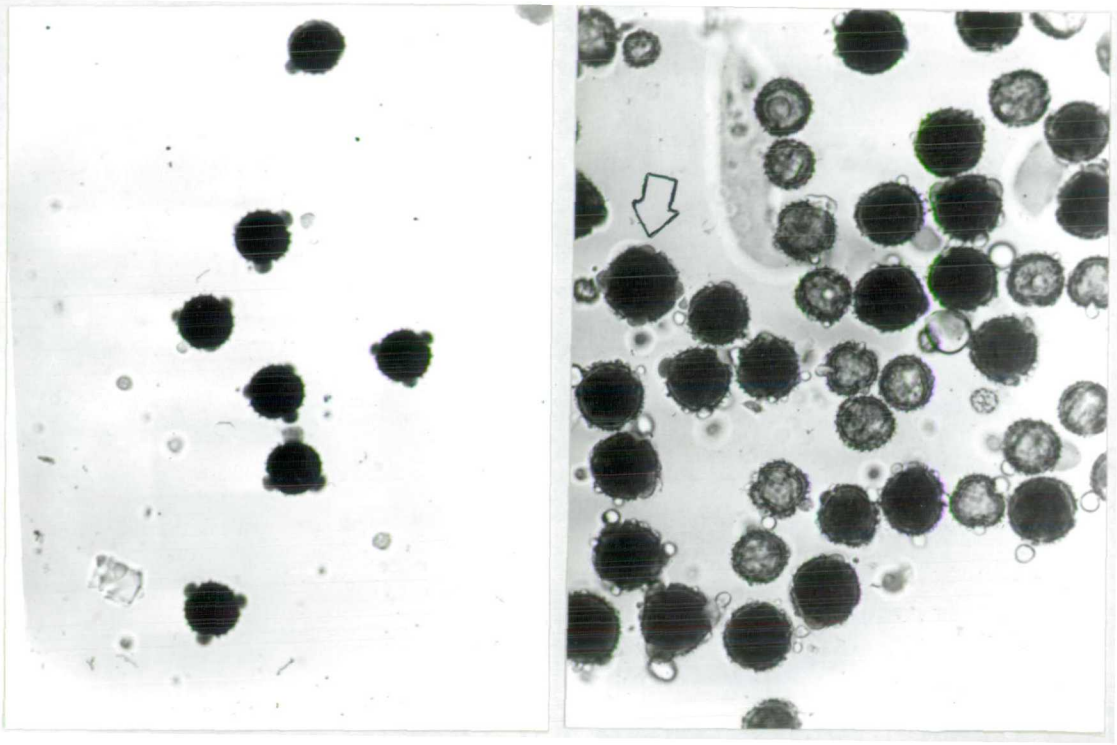

Plate A (X 280) Plate B (X 280)

Plate A

plant	status	pollen stained	diameter of stained pollen (mean, 95% limits and range)	comments
S29:4	diploid	97.9%	26.9±0.4 (25.1 - 30.7)μ	exclusively 3 pored

Plate B

CS12:7	C_1 auto-tetraploid	45.2%	34.3±0.4 (31.6 - 37.2)μ	both 3 and 4 pored (a 4 pored grain is arrowed)

Preparations were in both cases made in cotton blue/lacto-phenol.

Pollen stainability was in both cases assessed from counts of 400 - 500 grains. Pollen diameters were derived from 50 measured grains in S29:4, and 100 grains in CS12:7.

Table 29 Achene lengths (in mm.) of diploid and C_0 autotetraploid Senecio squalidus:

plant	2n =	no. seeds measured	mean	s.d.	range
DIPLOID					
S807:1:2	20	20	2.59	0.03	2.4 - 2.7
S807:r-	20	10	2.51	0.09	2.4 - 2.7
CS8	20	15	2.31	0.09	2.1 - 2.5
CS14	20	20	2.44	0.10	2.2 - 2.6
total		65	2.47	0.13	2.1 - 2.7
TETRAPLOID					
CS2	40	20	3.19	0.14	3.0 - 3.4
CS3	40	3	3.17	0.12	3.1 - 3.3
CS10	40	59	3.54	0.23	3.1 - 4.2
CS11	40	10	3.07	0.10	2.9 - 3.2
CS12	40	39	3.37	0.28	2.8 - 3.8
CS13	40	20	3.01	0.19	2.7 - 3.3
total		151	3.34	0.30	2.7 - 4.2

Note: All of these diploids shared the same maternal parent with all of the tetraploids. CS8 and CS14 received colchicine treatment at the cotyledonary stage, but remained diploid, CS8 was subsequently treated with colchicine in its axils and produced tetraploid branches (cf. Table 27).

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divided into two categories where homomorphic plants are concerned: gametophytic, where pollen function is controlled by its own genotype; and sporophytic, where pollen function is controlled by the genotype of either or both of the gamete-donating sporophytes. In both of these types of self-incompatibility systems, where pollen/style or pollen/stigma reactions are considered, usually multiple alleles (= S alleles) of a single gene are involved.

These two self-incompatibility systems function differently when the plants possessing them are rendered polyploid. Plants with the sporophytic multi-allelic system retain essentially

the same breeding system. Plants with the gametophytic multi-allelic system, however, are rendered self-fertile by polyploidy, presumably due to competition between the two copies of each S allele in the pollen when in the heterozygous state (Lewis, 1943, and 1947).

Brewbaker and Majumder (1961), Rowlands (1964), and Brewbaker (1967) have surveyed the distribution of the two types of self-incompatibility in Angiosperms. From their observations it is apparent that the different types of self-incompatibility follow clear phylogenetic sequences, with the two types being mutually exclusive in different taxa. The sporophytic type appears notably in the Cruciferae and the Compositae, both families lacking any gametophytic types. Investigations of the breeding system in the Compositae have included the species Parthenium argentium (Gerstel, 1950), Crepis foetidus (Hughes and Babcock, 1950), Cosmos bipinnatus (Crowe, 1954), Helianthus annuus (Habura, 1957), and Chrysanthemum cinerarioides (Brewer, 1968). In addition, there have been no reports in the literature of polyploidisation of Compositae (or Cruciferae) inducing self-compatibility. Many Compositae, including natural polyploids are, of course, self-compatible.

Colchicine treatment induces a degree of self-compatibility together with tetraploidy in the normally self-incompatible diploid S. squalidus. This behaviour is indicative of a gametophytic self-incompatibility system, which is at variance with the sporophytic system reported for other members of the Compositae.

In the C1 generation seed set under non-isolated conditions

was much reduced (down to about 5%), possibly due to increased gametic infertility. However, pollen stainability was maintained at about the same level (50 - 70%) as in the C_0 generation; and isolated plants set no seed. It appears, therefore, that the self-compatibility of the C_0 generation is not maintained in, at least, the C_1 generation. It is difficult to accompdate these observations within a purely genetic explanation.

Ascher (1966) suggested that, in a gametophytic self-incompatibility system, the S alleles produced monomeric regulators of pollen growth, which combined to form dimeric repressors if style and pollen regulator molecules were the same. He based his model on the operon theory (Jacob and Monod, 1961).

The sporophytic type of self-incompatibility differs from the gametophytic type in that in the former a factor affecting the pollen/style reaction may be transmitted cytoplasmically in the pollen. This factor is present in some form in the cytoplasm before the flowering process, for self-incompatibility can be removed by repeated back-crossing so that a nucleus is transferred to a new cytoplasm (Mizushima and Katsuo, 1958: using Brassica napus and B. campestris); or weakened in successive generations of cuttings (Blanchet, 1968: using Brassica oleracea). The sporophytic system may differ from the gametophytic system in that the operator molecules are only active when in the presence of the cytoplasmic factor. In both gametophytic (as in Trifolium:

Table 30

Chromosome segregation in pollen mother cells of C_0 autotetraploid Senecio squalidus:

plant code:	number of cells observed:	chromosome numbers at anaphase I: 20:20	19:21	18:22	segregation if micronuclei present:
CS 2	13	9	3	0	18+21+1
CS 8	15	10	4	1	
CS 12	6	3	1	0	19+19+2, 19+19+2
CS 16	14	12	1	1	
Total	48	34	9	2	3

Evans, 1960) and sporophytic (Theobroma: Addison and Taveres, 1952) systems a correlation has been shown between sexual incompatibility and graft incompatibility for different genotypes. This led Pandey (1967) to suggest that the S alleles can control other features besides the breeding habit, and are active and, therefore, can be affected very early in the sporophytic phase of the plant.

This provides an alternative explanation for the gametophytic system for Senecio squalidus suggested by the species' behaviour following colchicine-induced polyploid--isation. The colchicine used in rendering seedlings and axillary buds of S. squalidus polyploid may also have had the effect of partially inactivating the cytoplasmic factor necessary for the continuity of the expression of the incompatibility. Inactivation of the cytoplasmic factor would result in a pseudo-gametophytic self-incompatibility system, - the results of colchicine-induced polyploidisation, therefore, including self-compatibility. The lack of seed

set in the C_1 generation probably was due to restitution of the cytoplasmic factor governing self-incompatibility. This is supported by the slight seed set observed in the C_1 plants which must have been subject to cross-pollination.

Unfortunately, no observations were made of the breeding behaviour of the colchicine-treated plants which remained diploid.

The morphological effects of tetraploidisation of S. squalidus in the C_0 and C_1 generations are summarised in Table 31. It is notable that the morphological dis-similarities between tetraploid and diploid only appeared in the C_1 generation, together with the self-incompatibility. These are effects of colchicine polyploidisation which I have been unable to find reported elsewhere in the literature. Also presented in the Table are similar results obtained from the progeny of S. squalidus X S. viscosus.

The sex of the peripheral florets in both C_0 and C_1 generations of S. squalidus was female, as in the diploids. Tetraploidy per se does not, therefore, effect expression of sex in these plants.

It is apparent that a sexual cycle is necessary before the gigas characters of polyploidisation are manifested in S. squalidus and S. squalidus X S. viscosus. It is notable that the gigas effects persist into the second generation following colchicine polyploidisation of the S. squalidus X S. viscosus material, and therefore they probably do the same in generations of S. squalidus subsequent to the C_1. Possibly tetraploid and triploid individuals produced via non-reduction

Table 31 Morphological changes before and after the first sexual cycle following colchicine induced polyploidy in Senecio squalidus and S. X londinensis:

	PARENT:				PROGENY:		
plant code	ploidy (x = 10)	leaf size	ligule length (range in mm.)	achene length (range in mm.)	ploidy	leaf size	ligule length (range in mm.)
S. squalidus							
S31 EL1	2x	M	10.5 - 12.0	2.2 - 2.6	same as parental plants		
CS2 CS12	4x	M	11.5 - 12.5	2.8 - 3.8	4x	M	16.0 - 18.5
S. X londinensis							
S823 (13r)	3x	M	7.0 - 8.5	2.6 - 3.1	3x	very diverse	
					±5x	S	4.0 - 6.5
					±6x	L	10.0 - 11.5
S823 (13r) CS1 CS18 CS25	6x	M	8.5 - 9.5	2.9 - 4.6	± ±5x ±6x	L	10.5 - 13.5
CS7	6x	M	7.5 - 9.0	3.0 - 3.9	±5x	S	5.5 - 7.0
					±6x	L	10.5 - 11.0

Note: Leaf size, as used in this Table, refers to three readily recognisable sizes of middle cauline leaves under the conditions of which all of these plants were grown: S refers to leaves of about 4 cm. in length; M to about 6 cm.; and L to about 10 cm..

Diploid (2x) progeny of diploid S. squalidus is, of course, of the same type as the the parents; and triploid (3x) progeny of triploid S. X londinensis, presumably because of segregation of dissimilar genomic material do not resemble the parents.

of gametes under natural conditions would immediately express the gigas character.

The large size of the ligules in the C_1 S. squalidus renders them very conspicuous (see Plate 6). Potted examples of C_1 tetraploid plants, when transferred to a natural stand of ordinary S. squalidus were readily recognisable by virtue of their flower size from a distance of 20 - 30 metres.

The readily recognisable form of tetraploid S. squalidus, at least from these observations, makes it improbable that tetraploid populations could occur in nature without detection. The only report made of larger than normal ligules in the species was Druce's var. grandiflorus (from Botley, near Oxford, 1922: a specimen is in the Fielding-Druce Herbarium, OXF), which he described as having ligules 20 - 30% larger than normal in a note attached to the specimen. There is, however, nothing to suggest that the ligules approached the 16 - 18 mm. of the material described above, which represents an increase of up to 50% over normal. Additionally, pollen sizes in Druce's plant appeared to be of normal dimensions.

These results suggest that autotetraploidisation of S. squalidus is not responsible for the ligulate character appearing in S. vulgaris because: autotetraploidisation per se results in characters well removed from those necessary for morphological continuity between S. squalidus and S. vulgaris; and the conspicuousness of the autotetraploid, and their consequent apparent absence from nature makes it improbable that gene flow takes place from S. squalidus to

Plate 6 Diploid and tetraploid capitula of S. squalidus:

The plate is ½ life size, - the background scale being in cm..

The capitula on the left are from plant S807:1:2:4, a diploid with a mean ligule length of 12.1 mm. ± 0.13 mm. (range 11.9 mm. - 12.5 mm.); those on the right from a C_1 tetraploid, CS2:21, which had ligules of 18.4 mm. ± 0.25mm. (range 17.5 mm. - 19.0 mm.).

S. vulgaris via either occasional tetraploid individuals, or via established tetraploid populations.

2. INTROGRESSION VIA THE COMBINATION OF AN UNREDUCED S. SQUALIDUS GAMETE WITH A REDUCED S. VULGARIS GAMETE

The occurrence of large pollen grains, containing presumed unreduced chromosome complements, is fairly rare in S. squalidus. These grains occur with differing frequencies, both within and between S. squalidus plants of both British and Sicilian origin. This condition is distinct from the variable pollen sizes observed in the Sicilian S. squalidus,

where the larger grains are extremes in a continuous range of variability.

Most plants studied have not revealed large grains of this type, but I have recorded frequencies as high as 0.19% (9 in 4959 normal grains). These large grains give every appearance of otherwise being normal. They exhibit normal protoplasmic stainability and well developed germ tube primordia. Rarely four pores were seen instead of the usual three. That these grains may be unreduced is indicated by their similarities with pollen of autotetraploid S. squalidus.

Manipulation of naturally occuring unreduced pollen grains to fertilise S. vulgaris would be extremely difficult. Therefore, colchicine induced autotetraploid S. squalidus pollen was used.

Experimental crosses of S. vulgaris onto S. squalidus proved to be impossible, or virtually so (see Materials and Methods, pp. 246-251). Consequently pollen from both the colchi-autotetraploid S. squalidus plants and their first generation offspring (also tetraploid) were used to pollinate emasculated S. vulgaris. Despite repeated attempts, such fertilisations were unsuccessful, as they were with similarly prepared S. viscosus. It appears, therefore, that auto--tetraploid S. squalidus, despite its own induced self-incompatibility, cannot pollinate S. vulgaris, and indicates that the incompatibility system is probably not responsible for this barrier to hybridisation.

The occurence of triploid and tetraploid hybrids under natural conditions is dependent upon the amount of pollen

exchange taking place between the parental species; the competitiveness of the pollen on the alien styles; and the viability of the products of fertilisation (embryo, endosperm, and the developing plant).

S. squalidus and S. vulgaris often occur together, usually in disturbed habitats (waste ground; railway yards; etc.) and observation shows that Dipteran pollen carriers visit both species. Both species can be found flowering in almost any month of the year, and in the reduced competitive--ness of late autumn they may be subject to quite considerable visitation by insect pollinators. This is the time of year when, presumably as a result of deleterious environmental effects, I have noted a greater occurrence of large pollen grains.

Despite this, naturally occuring hybrids are very rare when compared with S. squalidus and S. viscosus growing together (this is discussed later in this Chapter, see pp. 156-161). The negative results do not eliminate the possibility that tetraploid hybrids occur in nature. The exact block (or blocks) to hybrid formation was not determined, and possibly different environmental, or different genotype combinations might be more successful.

3. INTROGRESSION VIA HYBRIDISATION BETWEEN SENECIO CAMBRENSIS AND S. SQUALIDUS

S. cambrensis was first described in 1955 (Rosser, 1955) from one locality in North Wales, whence its spread has been minimal. Despite its tendency to segregate slightly, the

Welsh material is still a readily recognisable taxon, even in its eligulate form, except when compared with material such as S602 (pp. 110-131). It is probable, therefore, that it never did occur in other localities than North Wales, for constant, albeit temporary, populations of S. squalidus/ vulgaris intermediates have not been recorded in other localities, and this is supported by the herbarium record.

The possibility exists that S. cambrensis could have arisen on more than one occasion, and in more than one locality, and could have segregated to the extent of being indistin--guishable from one or other of the parental species. As such, it could easily be overlooked as a distinct taxon. However, the relative constancy and intermediate nature of the Welsh S. cambrensis indicate that this would probably not happen.

The chromosome complement of the material of S. cambrensis still native to North Wales, which is described more fully in a later Chapter, appears to include a few with sub-terminal centromeres, - often about six are recognisable. Such chromosomes were not present in any of the S. squalidus plants which I have studied, and the majority of S. vulgaris plants that I have studied also lacked them. They are probably the result of re-arrangements of chromosome material following meiotic irregularities. Chromosomes of this type were seen in two of the S602 segregants, but were absent in the others which I studied. This indicates that they were probably absent from S602 itself, which in turn suggests that S602 did

Table 32 The incidence of sub-terminal chromosomes in Senecio vulgaris: (sub-terminal chromosomes has been abbreviated in the Table to s.t.c.)

locality collected	comments	no. plants studied	comments on karyotype
Brymbo, Denbighshire	var. hibernicus	4	2 s.t.c. per complement
Cambridge	var. hibernicus	2	no s.t.c. seen
Coxtie Green, Essex	var. hibernicus	5	2 s.t.c. seen in one plant
Tollesbury, Essex	maritime, eligulate race	1	no s.t.c. seen
Ainsdale, Lancashire	maritime, ligulate race	2	no s.t.c. seen
Staines, Middlesex	eligulate ssp. vulgaris	1	no s.t.c. seen
Oxford	eligulate ssp. vulgaris	2	no s.t.c. seen
	var. hibernicus (from experimental material of Canio Vosa)	6	2 - 4 s.t.c. per complement

Note: The Table includes only data from preparations in which mitotic metaphases were of sufficient clarity to allow conclusions on karyotype to be made.

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not arise by hybridisation between S. squalidus and the Welsh S. cambrensis.

I have seen similar chromosomes in some S. vulgaris plants, but never more than two per somatic complement. These plants included some that were from populations possessing the ligulate character or the well-dissected S602-type leaves previously described. Isolated, and presumably non-introgressed S. vulgaris appears to have none of this type of chromosome (see Table 32). The appearance of such chromo--somes in two of the S602 segregants supports their origin in meiotic irregularities, and their presence may be of use in

detecting introgressed populations of S. vulgaris.

The cross S. cambrensis ♀ X S. squalidus ♂ was successful. Difficulties with self-pollination precluded reciprocal crossing. The successful cross used emasculated S. cambrensis and S. squalidus as the pollen parent. The eligulate S. cambrensis (described in the next Chapter) was used, so that the ligulate character could be used as a genetic marker. Eleven heads of S. cambrensis were emasculated and periodically dusted with pollen from a S. squalidus plant. Nine seeds were set, all germinated, and the chromosome numbers of the young plants were determined. Seven of these nine resembled S. cambrensis in leaf shape, and all were at the hexaploid level, according to rough counts of their chromosomes (in all cases 2n = between about 56 and 60). These were therefore taken as being the products of self pollination. The other two plants resembled S. squalidus vegetatively, and rough chromosome counts of these plants showed them to be tetraploids (2n = about 38 - 40). Subsequent development, including floral morphology and fertility, of the latter plants was not assessed, but at least a small amount of seed was set.

Apparently, therefore, this mechanism for introgression is possible, but the localisation of S. cambrensis renders it highly improbable that this is the usual method.

4. INTROGRESSION VIA OCCASIONAL FERTILITY OF THE F_1 TRIPLOID HYBRID BETWEEN SENECIO SQUALIDUS AND S. VULGARIS

In terms of numbers of chromosomes, this appears to be the least neat, and therefore possibly the least probable alternative. However, Canio Vosa (personal communication) managed to hybridise S. vulgaris and S. squalidus, obtaining a single seed on the maternal S. squalidus which gave a hybrid, triploid ($2n = 3x = 30$) plant. Vosa described this plant as being large, with a great number of semi-pendulous, short-liguled capitula: indeed, "almost attractive". This hybrid in turn set a solitary seed, which gave rise to a plant which Vosa determined to be nearly hexaploid, with $2n = 57$. Vosa did not pursue this line of research further, but the $2n = 57$ plant was grown in the Oxford Botany School Gardens (now built over), and was fertile.

About two years later (in April, 1967), I found that the population of S. vulgaris occuring as weeds in these Gardens included ligulate, eligulate, fairly hirsute, and non-hirsute plants in all combinations, including the eligulate/ligulate heterozygote. All plants were of normal S. vulgaris dimensions (10 - 25 cm. in height), and their leaves ranged from those with triangular lobes to those with deep dissections and oblong lobes (cf. Figure 13, p.114). I determined that the chromosome number of eight of the progeny of these plants was $2n = 40$. The three different plants which gave rise to these progeny consisted of an eligulate, fairly hirsute plant and two ligulate ones, one of which was also fairly hirsute.

Pollen of these eight plants showed a slightly lower stainab-ility than might be expected in S. vulgaris (90 - 96% as opposed to 98 - 100%), but was of similar, although more variable dimensions (for example: 23.11 ± 2 S.E. of 1.41 μ as opposed to neighbouring S. vulgaris with 26.72 ± 0.49 μ). I have not seen ligulate S. vulgaris in other localities in and around Oxford during numerous visits.

I am of the opinion, which is shared by Vosa, that this S. vulgaris population includes the progeny of Vosa's hybrid. It is doubtful if as many as six generations had occurred between the introduction of the 2n = 57 plant and the situation in 1967, and a more probable maximum is four generations. The evidence for the actual introgression of S. squalidus genes into S. vulgaris is, of course, circumstantial in this case, but whether it is correct or not one other point is of interest, and that is the apparent failure of the near-hexaploid F_2 plant (with 2n = 57) to stabilise in subsequent generations at the hexaploid chromosome level, - equivalent to S. cambrensis.

My attempts to hybridise S. vulgaris and the diploid S. squalidus are described fully in Materials and Methods (see pp.246-251), but can be briefly summarised as unsuccessful. I consider this to be a very rare event in nature, and the implication of this is is discussed more fully on pp.138+240.

My studies in this direction have been limited to the similar hybrid S. squalidus X S. viscosus. The possibility has been discussed in the Introduction that the inbreeding, monocarpic tetraploid Annui had a monophylogenetic origin.

The similarities between S. viscosus and S. vulgaris are considerable, and the two species are probably closely related. Apparently they are reproductively isolated by the failure of hybrid embryos to develop (Gibbs, P.E., personal communication), and possibly this isolation has resulted in an evolutionary divergence between the two species which is reflected more in their morphology than in genomic differentiation.

The F1 hybrid of S. squalidus and S. viscosus is considerably easier to synthesise, and much more common in nature than is S. squalidus X S. vulgaris. All three species are common, and occur in similar habitats, although S. viscosus tends to be more local than the other species, and S. viscosus pollen resulted in quite considerable production of hybrids, as well as selfs; but pollination with S. vulgaris, even when it was certain that some pollen had been transferred, induced only self-pollination. Presumably S. viscosus pollen is competetive with that of S. squalidus on the latter species' styles, whereas pollen of S. vulgaris is not.

An interesting point is that the introgression of genes into S. vulgaris from S. squalidus may bring about an increase in pollen production in the former species (cf. the S602 segregants). Another is that hybridisation is possible using S. squalidus pollen when the recipient has a hybrid origin involving S. squalidus. Thus, S. vulgaris cannot be hybridised using S. squalidus pollen, but S. cambrensis can, and so can the male sterile, ligulate S. vulgaris plants used

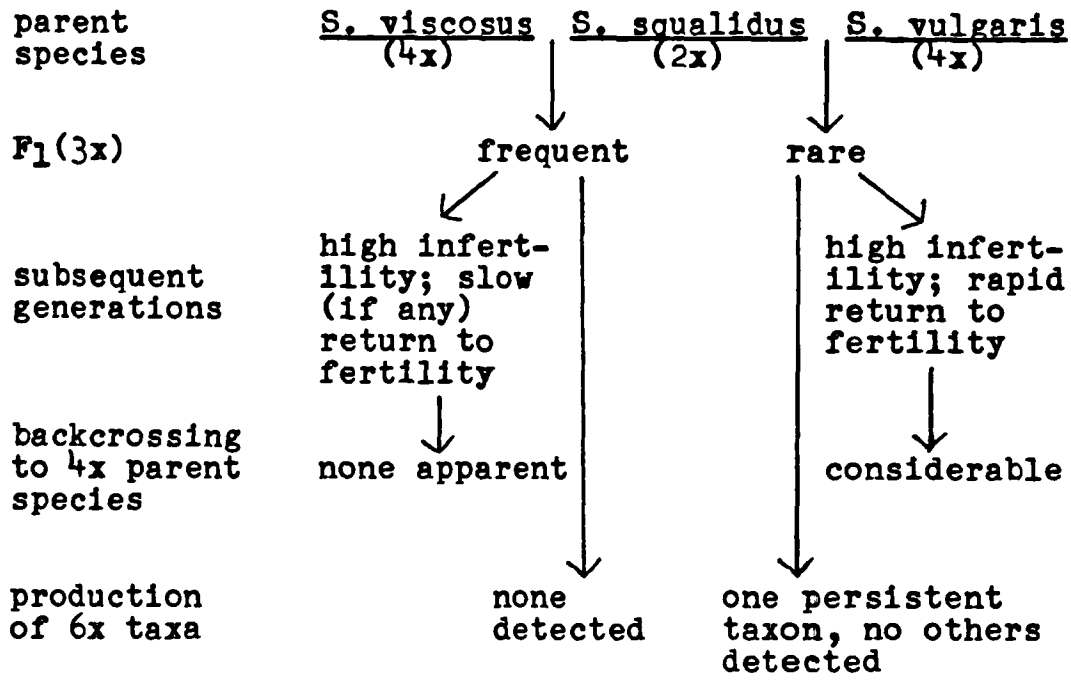
by Trow (1912) and Harland (1954) - see pp. 163-164. Possibly as introgression proceeds from S. squalidus there is an increase in pollen available for further hybridisation in S. vulgaris, and a decrease in incompatibility between S. squalidus pollen and S. vulgaris styles. Is it possible that the introgression rate from S. squalidus into S. vulgaris has been increasing, and will increase further? This may explain why the four centres of evolution of S. vulgaris var. hibernicus up until 1900 are so clearly marked, with an increase in the ease of hybridisation succeeding each hybridisation.

Full details of S. squalidus X S. viscosus and their hybrid families are given in the Chapter dealing with Senecio X londinensis. The main feature of this study is that the eventual progeny from the triploid and colchi-hexaploid F_1 hybrid tend towards two chromosome levels - tetraploid and hexaploid, in both cases with increases in fertility.

Obviously, extrapolation from the situation with S. squalidus X S. viscosus to S. squalidus X S. vulgaris is liable to give erroneous conclusions, but a certain amount of circumstantial evidence from the latter situation correlates with the former. They both form triploid hybrids, and can both form tetraploid and hexaploid families of hybrid origin (see Figure 18). The main differences lie in the far greater frequency with which the hybrid S. squalidus X S. viscosus is formed, and the noticeable introgression of genes into S. vulgaris and not into S. viscosus. My experimental material shows that the S. squalidus/S. viscosus intermediates apart from the F_1 hybrid are easily recognisable, and yet they

Figure 18

Genetic continuity between Senecio squalidus and S. vulgaris and S. viscosus:



only appear very rarely, if at all, in the field or the herbaria. One must assume that the block to introgression from S. squalidus into S. viscosus occurs because of the infertility of the hybrid families, although the lack of apparent introgression may be due to no S. squalidus genes with recognisable effects persisting in S. viscosus. With S. squalidus and S. vulgaris the intermediates appear to possess a high degree of fertility, and so from the point of view of potential introgression the rarity of F_1 hybrids is overcome by the establishment of these families. An interesting, and possibly significant parallel to this is

that despite the relative frequency of spontaneous S. squalidus X S. viscosus F1 hybrids, no natural allohexaploids have been detected, in contrast with S. squalidus X S. vulgaris, where the allohexaploid hybrid S. cambrensis has become established.

To carry a stage further the extrapolation of data from S. squalidus X S. viscosus to S. squalidus X S. vulgaris: the former apparently showed a tendency for the functional gametes formed to include approximately multiples of the basic haploid (n = x = 10) chromosome number (this is discussed in detail in the Chapter on Senecio X londinensis). Thus, a triploid (2n = 30) could give rise to gametes with n = about 10, 20, or 30, which was reflected in its progeny having somatic chromosome numbers of about 30, 50, and 60. Similarly, a hexaploid gave rise to pentaploids and hexaploids, and was therefore presumably producing gametes with n = about 20 and 30. If an analogous situation exists in S. squalidus X S. vulgaris, it is easy to see how Vosa's triploid F_1 hybrid gave rise to a nearly hexaploid plant, which might have been responsible for rapid introgression into S. vulgaris by producing tetraploid, or even pentaploid offspring. Such a process could explain the tetraploid hybrid S602. It is of interest to note in this context that the herbarium record for S. cambrensis-type plants in North Wales goes back to at least 1910, or even 1868 (see Appendix Table 4). North Wales was one of the centres of origin of S. vulgaris var. hibernicus, probably in about 1900. Could it be that a single triploid S. squalidus X S. vulgaris hybrid gave rise to stable

populations of both hexaploids and tetraploids at the same time by the production and combination of, respectively, gametes with n = 30 and 20?

THE TAXONOMY OF SENECIO VULGARIS VAR. HIBERNICUS

It is established that the ligulate character in S. vulgaris is controlled by a single gene. The gene is not apparently linked with other recognisable characters, despite its postulated origin in introgression from S. squalidus. As such, the character only merits recognition as a forma, and the nomenclature of D.E. Allen (in Perring, 1968) should apply. Thus, the non-maritime ligulate races of S. vulgaris should be refered to as ssp. vulgaris forma ligulatus D.E. Allen.

Plants, such as the S602 family, which are early stages in the introgression sequence must normally be treated as nothomorphs. However, it is possible, and indeed may have been the case with D.P. Young's "giant rayed groundsel", that these taxa may stabilise as self maintaining, morphologically intermediate lines by segregation, as opposed to back-crossing into S. vulgaris. As such, these lines will possibly show greatest morphological affinity to S. cambrensis, although in terms of genetic continuity their closest relative will be S. vulgaris. Until the persistence (if any) of these lines in nature is established no taxonomic treatment can be given to them.

A NOTE ON MALE STERILE PLANTS OF SENECIO VULGARIS

There have been two recorded instances of male sterility in S. vulgaris.

Trow (1912), in one of his hybridisations involving a ligulate variety, obtained spontaneously a pollen sterile plant with "fimbriate" ligules. The fimbriate character was caused by the ligules being very deeply divided. Trow showed that the paired characters of fimbriate ligules and male sterility were inherited together through four generations.

Harland (1954) used another ligulate, male sterile plant of S. vulgaris named "dwarf strap" , progeny of which he utilised in the artificial synthesis of S. cambrensis. Plack (1952) described the dwarf strap line as being slow growing, easily diseased, with small, narrow leaves, long, narrow ligules (when present), and long, pointed, narrow involucral bracts. Other characters varied according to the crossing programme. The male sterility was due to abortion of the anthers, and the plants were female fertile. Plack suggested, from her genetic analysis, that the dwarf strap characteristics might be the result of four recessive mutant genes.

In both of these cases the male sterility has been genetically controlled and has been associated both with the ligulate character, and with morphological abnormalities. The multigenic control suggested by Plack would indicate that dwarf strap was less probably a product of chance mutation than the result of genic or endo-phenotypic unbalance. This unbalance might have been caused by hybridisation involving a functionally

different genotype. It is relevant to note that the S602 family segregated for several morphological characters similar to those shown by dwarf strap. These included disease (mildew) susceptibility, weak and straggling growth, abnormal leaf shapes, and, occasionally, a degree of fimbriation of the ligules. The possibility exists, therefore, that both Trow's fimbriate type and Harland's dwarf strap are products of the introgression sequence from S. squalidus into S. vulgaris, although in the S602 family complete male sterility was not encountered.

SENECIO VULGARIS VAR. DENTICULATUS

The coastal taxa of S. vulgaris are diverse and often not easily separated from others of the species. The best known, and most easily recognised of these varieties is var. denticulatus (O.F. Muell.) Hyland (= ssp. denticulatus (O.F. Muell.) P.D. Sell).

In general var. denticulatus has small ligules; is arachnoid-hairy; and has leaves amplexicaul, and spathulate to laciniate. In its natural habitats (such as sand dunes, and coastal cliffs) it usually has an erect habit with only few or even solitary capitula, and with leaves small and widely spaced on the stem. The capitula often show considerable reduction in floral part numbers when grown in adverse conditions. When in cultivation the plants grow more profusely with larger leaves and increased numbers and often increased size of capitula due to an increase in floral part number. The hirsute nature of the plants is amplified, although this may be due to the lack of abrasion and desiccation of the leaf and stem hairs under cultural conditions. In addition, the taxon is very susceptible to mildew (Erysiphe spp.) when grown in the humid conditions of a glasshouse.

The coastal taxon apparently can intergrade with the non-coastal var. vulgaris. This was reported by Lange (1851) in Bornholm, and by Wilmott(1925) for a hirsute coastal population in Sussex. In addition, herbarium specimens from the Channel Islands (in CGE, BM, K, and OXF) show a range of intermediates

between vars. vulgaris and denticulatus.

Other maritime taxa can be recognised. Thus, ligulate plants resembling var. denticulatus can be found on the coastal dunes between Liverpool and Southport (Lancashire). These plants differ mainly from var. denticulatus in being less hirsute. In cultivation they are characterised by their mildew susceptibility, and a tendency to form a distinct basal rosette of leaves before producing relatively unbranched flowering stems. The rosette forming character prompted C.D.K. Cook (personal communication) to suggest that these plants were biennial. I have found no indication that these plants may have their bienniality controlled by photoperiodism, or that vernalisation is necessary for flowering, this being based on the uniformity of behaviour of the plants when grown in different seasons in a constantly heated glasshouse. It may be that the rosette habit is an overwintering stage on the dunes, flowering being induced by increasing temperature in spring. The seed thus produced would be able to survive the arid conditions of the dunes in summer, with seed germination being followed by the formation of the over-wintering rosettes. Certainly, during early June of 1967 the plants at Southport were in the final stages of seed production before death. V.A. Matthews (personal communication) has also noted the occurrence of two rosette-forming races of S. vulgaris, which she suggested might have been biennial. Her plants probably originated from the Lancashire dunes. Plack (1952) also worked with two rosette-forming races, both of maritime origin,

one from Caenarvon, and the other from Castletown, Isle of Man.

Eligulate maritime taxa also occur in the coastal regions of Wales, Scotland, and Ireland. All of these minor variants which have been investigated by me have been self-compatible, monocarpic, and tetraploid (2n = 40).

It appears from Table 33 that var. denticulatus is only the most readily recognisable of several maritime biotypes. It is, perhaps, to be expected of an inbreeder having habitat specificity that disjunct populations might show adaptive as well as non-adaptive differences. R. Abbott and J. Antonovics (unpublished data), working with S. vulgaris, have suggested that inbreeding taxa are capable of very precise adaptation to their habitats. The races occuring in sandy maritime habitats, where extremes of nutrient status, drought, accretion, salinity and exposure occur must be adapted to these adverse conditions, and on the basis of the work of Abbott and Antonovics are probably selectively maintained as discrete populations.

Probably, therefore, "var. denticulatus" refers to a number of maritime races which have some characters in common due to the effects of selection.

Several similar cases have been reported from the British flora. Of the two subspecies of Daucus carota L., ssp. carota is widespread and common, while ssp. gummifer Hook. f. is a coastal taxon which varies morphologically in different localities and intergrades completely with ssp. carota (Perring, 1968). Similarly, in Calystegia sepium (L.)R.Br., ssp.

Table 34

Types of maritime races of Senecio vulgaris:

✓ = character present; (✓) = character present in reduced form; - = character absent

(a) Live material:

locality	ligulate	hirsute	"denticulatus" type leaves	2n=	comments
dunes south of Southport, Lancs.	✓	(✓)	✓	40	basal leaves form rosette
dunes at Morfa Harlech, Merioneth	-	(✓)	-	40	closely resembles ssp. vulgaris
dunes, Guernsey	✓	✓	✓	40	ssp. denticulatus
dykes of salt marsh, Tollesbury, Essex	-	-	-	40	dwarfed biotype of ssp. vulgaris
(b) Herbarium material:					
				Hb.	
dunes between Liverpool and Southport, Lancs.	✓ ✓	- (✓)	✓ ✓	CGE MANCH LIV LIVU OXF SPT	occasionally occuring with large capitula; occasionally with dwarfed habit; rosette habit not apparent in Hb. specimens
dunes, Jersey	✓ ✓ - ✓ -	✓ ✓ ✓ ✓ ✓	(✓) ✓ - - ✓	CGE MANCH BIRM BM	occasionally occuring with large heads

- continued -

dunes, Guernsey	- ✓ - ✓ ✓ ✓ ✓	- ✓ ✓ (✓) (✓) - -	✓ ✓ ✓ (✓) - ✓ -	CGE MANCH BIRM K LIVU BM OXF	one specimen in possesses a distinct rosette
coastal, Weymouth, Dorset	-	✓	✓	BRISTM	
coastal, Tregantle, Cornwall	✓	-	✓	MANCH	
coastal, Teignmouth, Devon	✓	(✓)	(✓)	CGE	
dunes, Caithness	-	-	✓	CGE	
coastal, Killarney	✓	-	-	CGE	ssp. vulgaris var. hibernicus
coastal, Penarth, Glamorgan	✓	-	-	CGE	ssp. vulgaris var. hibernicus
coastal, Bressay, Shetland	-	(✓)	-	CGE	large capitula
coastal, Shetland	-	-	-	K	very large capitula
coastal, Seaton Sluice Northumberland	-	(✓)	(✓)	CGE	
coastal, Brean Down, Somerset	-	✓	(✓)	CGE	
coastal, Mweenish Is., Co. Galway	-	-	(✓)	DBN	very large capitula
coastal, Holywood, Co. Down	-	-	-	DBN	large capitula
coastal, Elly Bay, Co. Mayr	-	-	(✓)	DBN	dwarfed
coastal, Frassaro Bray (?), Co. Wicklow	-	✓	-	DBN	
coastal, Baldoyle, Co. Dublin	-	(✓)	-	DBN	large capitula

- continued -

Irishdaros, near Roundstone, Co. Galway	-	-	(✓)	DBN	large capitula
coastal, Lizard, Cornwall	-	-	-	K	large capitula, leaves said to be fleshy
coastal, Isle-of-Wight	-	✓	-	K	dwarfed plants with large capitula

(c) Reports from the literature:

locality	source	comments
coastal in the Isle of Man, Lancashire, North Wales, and south Devon	Perring and Sell (1968)	reported as ssp. denticulatus P.D. Sell
coastal in Jersey, Guernsey, Freshfield (Lancs.), Highbridge (Glos.), Bournemouth (Hants.), and Bigbury (Devon), and Tregantle and Whitsand Bay (Cornwall)	Rep. Bot. Exch. Club 1875:19; 1876:22; 1910: 568-570; 1927:264; and 1930:351 Rep. Watson. Bot. Exch. Club 1898/9:13; 1912/3: 395 Trimen (1897)	usually reported as var. radiatus, but localities suggest maritime races; the reports sometimes mention large capitula, dwarf habit, and hairiness
coastal cliffs, Bigbury (Devon)	letter on Hb. specimen in CGE from E.S. Marshall	reports plants at Bigbury as being dwarfed, ligulate, fairly hairy, and with leaves apparently of the denticulatus type
Pevensey shingles, (Sussex)	Wilmott (1925)	records eligulate, hirsute biotype (as S. lanuginosus Trow) hybridising with non-hirsute type

roseata Brummitt is a plant of western dunes in Britain and north-west Europe, which intergrades completely with the non-coastal ssp. sepium (Perring, 1968). Until recently in the genus Arabis, A. brownii Jord. was regarded as an endemic of the west Irish dunes with hairs only on the leaf margins; and the inland weedy A. hirsuta (L.) Scop. had hairs all over the leaves. More recent studies have revealed intermediates of these two types, including brownii-type hirsuta plants on the Pembrokeshire coast (Clapham et al, 1962), more hairy brownii plants on the Irish dunes, and less hairy, even glabrous, "hirsuta" plants in inland localities (B.M.G. Jones, personal communication). Jones (1963) suggested that the hairy/glabrous character was under the control of a single gene; and he separated on ecological grounds the two taxa into A. hirsuta ssp. hirsuta (inland) and ssp. ciliata (coastal), with local variants being recognised at the varietal and formal levels.

In each of these cases a coastal ecotype intergrades with a widespread inland taxon, while retaining its overall identity for sufficient of its morphological range to be recognised at the subspecific level.

Gene flow probably takes place between adjacent populations of Senecio vulgaris, as is indicated by the inherent variability found by Abbott and Antonovics within their isolated populations. Certain characteristics of these populations were, however, selectively maintained. It is probable that fairly rigid selection exists between maritime and inland habitats. Inland races are probably not well adapted to the extremes of the dune

habitats. The inland habitats where S. vulgaris is particularly common (that is, on disturbed agricultural soils) probably operate an overall weak selective pressure, but the great mildew susceptibility shown by dune races when in cultivation may render them unsuitable for these more "favourable" growing conditions.

Table 33 gives details of the maritime races of S.vulgaris which I have examined. It can be seen that these races, with a few exceptions, possess at least some of the characteristics of var. denticulatus, and in addition a few form basal leaf rosettes. As a group, and occasionally as an individual population; they intergrade with var. vulgaris. The var. denticulatus is only one readily recognisable taxon out of a spectrum of maritime biotypes. These biotypes as a whole should be given taxonomic ranking because of the range of characters by which they differ from var. vulgaris. I suggest, in view of the widespread and usually recognisable nature of the maritime S. vulgaris as a single, comprehensive taxon throughout Britain and Europe, that subspecific ranking is appropriate. The denticulatus taxon should, in view of its recognisability in both southern Britain and Europe become a variety of this maritime subspecies. Other recognisable biotypes should, as information accrues about them, be classed as further varieties, or as formae.

The taxon which I intend to constitute the subspecies displays several characters which may be additional to or absent from the subspecies denticulatus as outlined by Sell (in Perring,

1968, and as Sell, 1967). Where the circumscription of an infraspecific taxon is altered the International Code of Botanical Nomenclature suggests that the correct procedure is for the taxon to be emended. Thus, the maritime taxon becomes S. vulgaris ssp. denticulatus (O.F. Muell.) P.D. Sell emendavit P. Crisp. This subspecies consists of maritime taxa which may or may not differ from the non-maritime taxa by displaying any of the following characters:

1. ligulate peripheral florets
2. large capitula
3. "denticulatus"-type leaves: i.e. leaves with large auricles, semi-circular lobes, spathulate/oblong outline, and regular marginal dentation
4. green parts arachnoid-hairy (due mainly to "club" trichomes)
5. rosette of basal leaves (possibly an overwintering stage)
6. environmental effects often include a dwarf habit, and reduction in size and numbers of leaves and capitula.

THE POSSIBLE ORIGIN OF SENECIO VULGARIS VAR. DENTICULATUS

Strong circumstantial evidence suggests that S. vulgaris has been the recent recipient of introgressed genes from S. squalidus. An analogous situation may exist between S. vulgaris and S. vernalis W.& K.. The centre of origin of S. vernalis was probably in south-east Europe, where it occupied coastal and montane habitats. It is now widespread in the temperate regions of the Old World, often occurring as an anthropochore.

I have investigated samples of S. vernalis from Turkey, Iran, Yugoslavia, and Britain (where it is a rare introduction). All of these plants were very similar: they were self-incompatible, monocarpic diploids (2n = 20); they formed a basal rosette of leaves prior to producing a much branched, erect, sparsely leaved, flowering stem; they were arachnoid-hairy; and they possessed less than the normal number of 13 ligules per capitulum found in the diploids.

Three types of leaf trichome occur in the species of Senecio which I have investigated (see Materials and Methods, pp. 167-271). All three types are present in S. squalidus, - both British and Sicilian, in S. vulgaris, and in S. vernalis. Usually S. vulgaris has a low density of all three types of trichomes, but the maritime races of S. vulgaris from Guernsey and the Lancashire dunes (cf. Table 33) appeared to have a disproportionately high density of the "club" trichomes when compared with all other species investigated, except S. vernalis.

Unfortunately, I made no quantitative measurements of this character.

Leaf shape is a taxonomic criterion in many of the maritime races of S. vulgaris. Similarities exist between the typical "denticulatus" leaf and that of S. vernalis in the outline shape of the leaves, which tend to be spathulate/oblong; the high degree of auriculation of the leaves; the triangular/semi-circular shape of the leaf lobes, which are nearly at right angles to the leaf axis; and the regular dentation of the leaf margin. Some of these features are shown in Figure 19.

These similarities between S. vernalis and certain of the maritime S. vulgaris races, together with a comparison of S. vulgaris ssp. vulgaris are given in Table 34. They suggest three possibilities: that parallel evolution has taken place, possibly under the influence of the maritime habitat; that S. vernalis is directly ancestral to the maritime S. vulgaris; or that introgression has been taking place from S. vernalis into the maritime S. vulgaris.

If S. vernalis is ancestral to S. vulgaris, then an evolutionary link has been found between a monocarpic diploid and a monocarpic tetraploid. The possible evolutionary sequence might then have been: the diploid S. vernalis undergoes tetraploidisation and becomes a self-compatible taxon, and evolution at the tetraploid level proceeds to give a series of species with a reduced size of ligules,

Figure 19 Leaf outlines in Senecio squalidus, S. vulgaris, and S. vernalis:

A = S. squalidus (S807:1:2:3);
B = S. vulgaris var. hibernicus (S807:1:1);
C = S. vulgaris ssp. vulgaris (S95:3)
D = S. vulgaris ssp. denticulatus (G3:1);
E = S. vernalis (GM6).

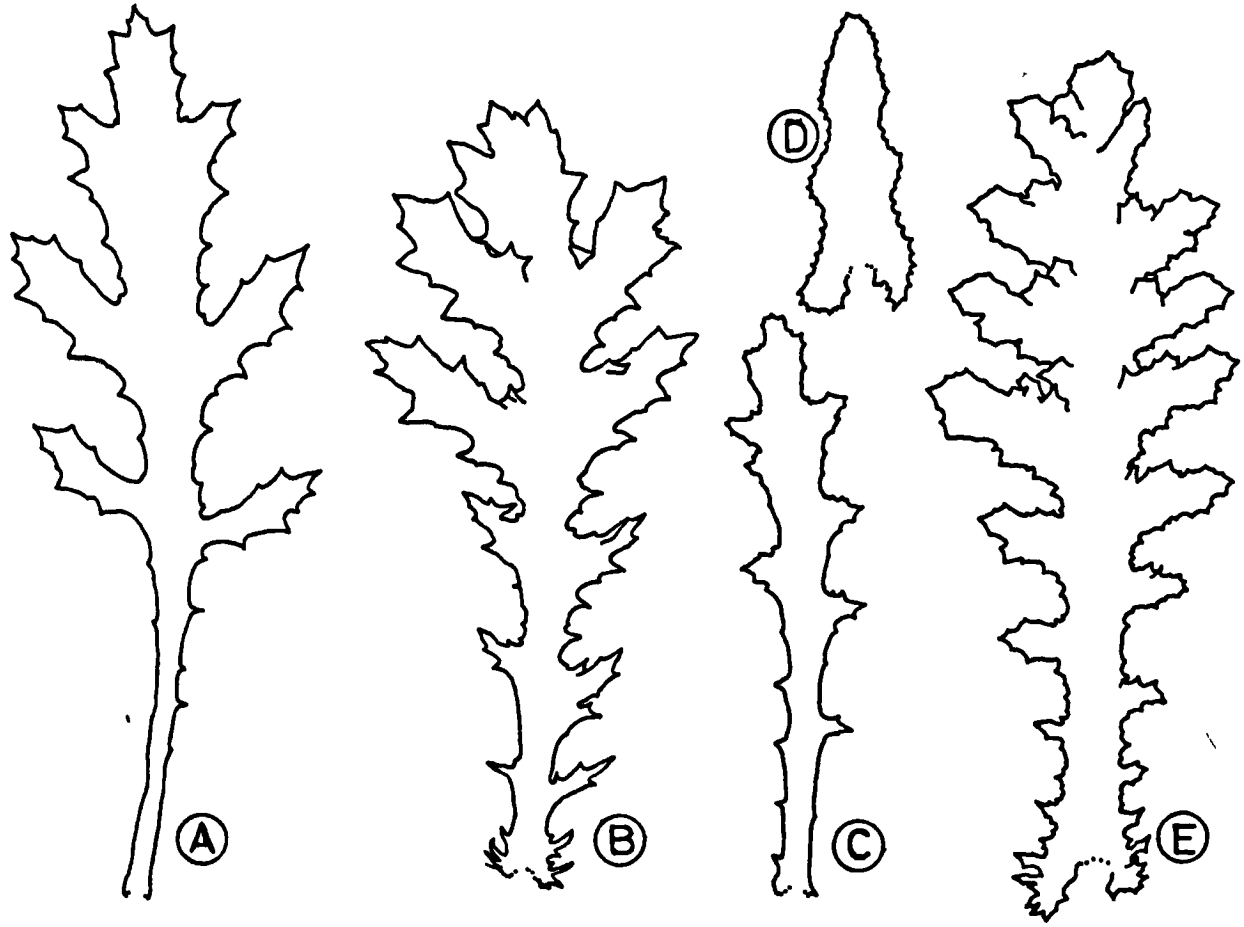


Table 35

Comparison between ligulate biotypes of Senecio vulgaris, and the diploid species S. squalidus and S. vernalis:

		S. vernalis	S. vulgaris var. denticulatus	S. vulgaris f. ligulatus	S. squalidus
2n =		20	40	40	20
habit		monocarpic annual, rosette forming	monocarpic annual, occasionally rosette forming (and overwintering as a biennial?)	monocarpic annual, erect or straggling	polycarpic annual/perennial, erect or straggling with a persistent ground level stem
habitat		coastal; montane; and weedy	coastal	weedy	montane; and weedy
distribution		Temperate; Old World	North West Europe	North West Europe	South Italy and Sicily; established in Britain
middle cauline leaf shape	lobes	semi-circular	semi-circular to triangular to oblong	triangular to oblong	oblong, leaves sometimes bi-pinnatifid
	margins	regularly dentate	fairly regularly to bidentate	usually irregularly dentate	irregularly dentate to bidentate
	auricles	large	often large, but otherwise variable	variable in size seldom large	variable in size, usually small in the British taxon
	outline	oblong	oblong to spathulate	oblong to rhomboid	oblong to rhomboid
hairiness		arachnoid-hirsute	more or less glabrous to arachnoid-hirsute	glabrous to slightly hirsute	glabrous to slightly hirsute

- continued -

		vernalis	*denticulatus*	*ligulatus*	*squalidus*
trichomes		mainly clubs	mainly clubs	as many whips as clubs	as many whips as clubs
capitula		in loose upright cluster	often in upright cluster, but also borne singly in adverse habitats	in tight, usually drooping cluster	loosely or singly on upright stalks
		large, bell shaped	often large, usually cylindrical, but occasionally with a slight bell shape	small and cylindrical	large, bell shaped
ligule	length	8 - 11 mm.	about 5 mm.	3.5 - 5 mm.	9 - 13 mm.
	number	8 - 10 (-13)	8 (-12)	8 - 13	usually 13
	reflexion	curl from base: 	various: some are as *S. squalidus*; others are non-reflexing: 		whole ligule curls round outer surface: 
mildew susceptibility		slight	extreme	slight	slight
leaf miner susceptibility		resistant to attack	resistant to attack	variable degrees of resistance to attack	extremely susceptible
breeding system		self incompatible and outbreeding	self compatible and inbreeding (and outbreeding possibly)	self compatible and inbreeding	self incompatible and outbreeding

and an increase in the glandular habit.

Some evidence does, however, exist that at least some ligulate races of S. vulgaris may have originated as a product of introgression from S. vernalis. S. vernalis has probably spread extensively in Europe in the fairly recent past (Ascherson, 1862; Kloos, 1952). To a large extent its present distribution in north-west Europe is similar to S. vulgaris ssp. denticulatus, except that it is often inland as well as coastal. A number of anomalous taxa have been described, of a nature intermediate between S. vernalis and S. vulgaris, including the sterile (presum--ably triploid) hybrid (Vatke, 1874; Jacobasch, 1894; and specimens in European sections of the Hb. MANCH, BM, and LIVU). I have only seen one series of specimens apparently involving S. vulgaris and S. vernalis which resembles my S602 material (that is, fertile segregants of S. vulgaris X S. squalidus). These were pressed specimens exhibited by G. Messenger*, gathered from a single locality, together with the introduced S. vernalis, from Rutland in 1967 and 1968. In support, Messenger (personal communication) stated that he and P.D. Sell had divided these specimens into two groups: those indubitably S. vernalis; and those of an intermediate nature between S. vernalis and S. vulgaris - these latter also being fertile.

* Botanical Society of the British Isles Annual Exhibition Meeting in London, November, 1968. Specimens are now in CGE.

SENECIO CAMBRENSIS

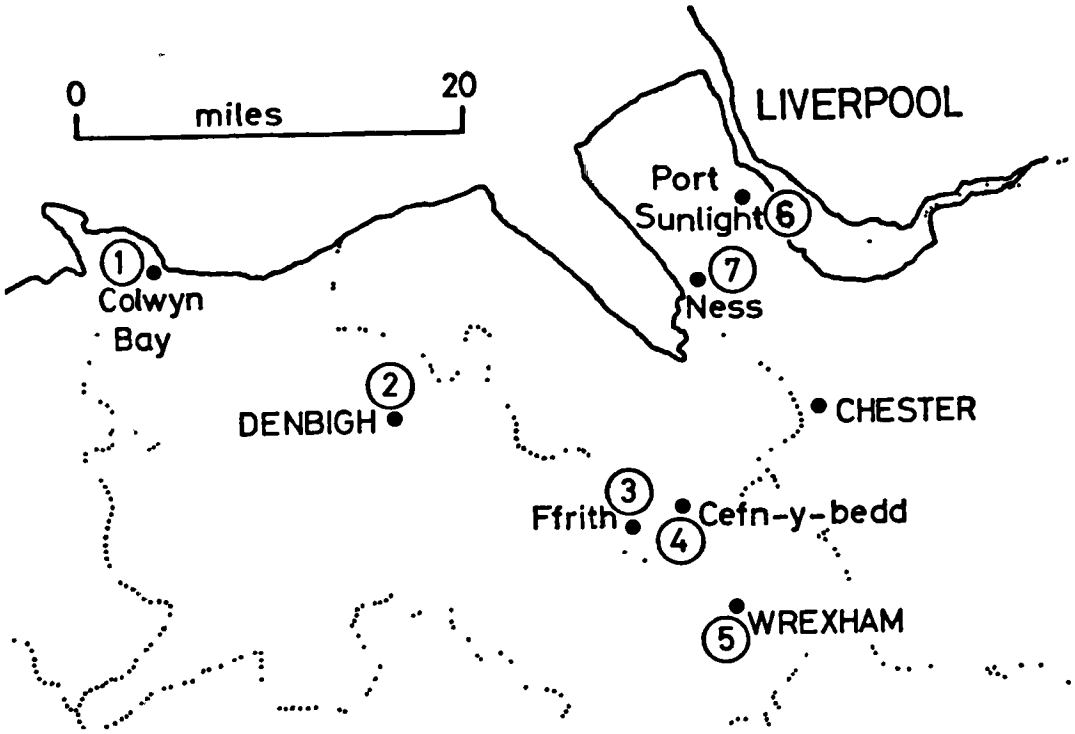
Senecio cambrensis was first described by Rosser (1955). She afforded it the rank of species, and stated that it was the allohexaploid (2n = 60) hybrid between S. squalidus (2n = 20) and S. vulgaris (2n = 40). This was supported by the work of Harland (in Rosser, 1955; and in Lousley, 1955), who used S. squalidus to pollinate a male sterile S. vulgaris plant (the "dwarf strap" plant already discussed, - see pp. 163-4). The resulting F_1 triploid was rendered hexaploid with colchicine, and was reported to resemble the natural S. cambrensis.

Definite records of S. cambrensis in the field originated about 1948, when H.E. Green (personal communication; and in Rosser, 1955) noted the plant near Ffrith, Flintshire, four miles north west of Wrexham, Denbighshire.. Green continued observations on the plants until 1953, when his donation of specimens to the Manchester Museum (MANCH) culminated in Rosser's paper.

The species, while not common around Ffrith, can be found with little difficulty, occupying cracks in walls and quarry-sides, and occasionally in disturbed soil. It has apparently only spread slightly from its original station. The only recorded occurences of the species far away from the Ffrith area (see Figure 20) are in the vicinity of Green's garden, at Ness, Cheshire, and at Colwyn Bay. The species is maintained at a number of botanical institutions (such as the Botanic Gardens of Cambridge and Edinburgh Universities),

Figure 20

Records of Senecio cambrensis:



1. Colwyn Bay, Denbighshire: in Nature in Wales 2(1) (1968) det. J.M. Brummitt and P.M. Benoit.

2. Denbigh: 1925 in OXF, collected as S. squalidus X S. vulgaris, det. as S. cambrensis by Rosser in 1957.

3. Ffrith, Flintshire: 1948, in CGE, - one of H.E. Green's specimens; 1954, several specimens in MANCH; 1955, in BM; 1956, in CGE, and MANCH; 1961, in LIVU; 1967 and 1968, collected by myself, and discussed in text: - included eligulate plants.

4. Cefn y bedd, Flintshire: 1948, in MANCH, det. by Rosser.

5. Wrexham, Denbighshire: 1968, in CHR, discussed in text: - eligulate plant.

6. Port Sunlight, Cheshire (apparently of the stock established by H.E. Green at Ness, - see 7.): 1967, in LIV, although I could not distinguish the herbarium specimen from S. squalidus.

7. Wirral, Cheshire (hort. ex Ffrith, in Green's garden at Ness, Neston): 1948, in BM, - one of Green's specimens; 1955 and 1958, several specimens in LIV; 1958, in SPT.

usually as teaching material, but no reports have been made of the species occuring as an escape from these institutions.

The herbarium record of S. cambrensis prior to Green's investigation possibly consists only of a single specimen collected from Denbigh by a Mr. Jones in 1925 (OXF). Originally identified as S. squalidus X S. vulgaris, Rosser re-named it as S. cambrensis in 1957. I cannot, however, distinguish between S. cambrensis and the S602 - type of plant (i.e. fertile, tetraploid S. squalidus/vulgaris intermediates) in this case. Reference to Figure 12a and Appendix Table 14 shows that a number of possible S602 - type plants were reported from this area prior to 1930, but the Denbigh plant, of all these, is indistinguishable from the modern S. cambrensis. The question must remain open as to whether S. cambrensis originated prior to 1948, or prior to 1925.

Rosser's description of S. cambrensis is comprehensive and accurate, and only requires enlargement in the aspects discussed below.

On herbarium specimens (MANCH, OXF, and CGE) all collected in 1956 from Ffrith, Rosser has noted the occurence of "long", "medium", and "short" liguled plants of the species. From these herbarium specimens it appears that the "short" liguled plants are probably of the only class that Rosser described in her 1955 paper, - that is, about 4.8 mm. in length. The "long" ligules are probably about 8 mm., and the "medium" ligules about 6 mm.. In my experience it is within this range (i.e. about 5 - 8 mm.) that S. cambrensis

is represented in those cultivated stocks already referred to. Around Ffrith, in 1967 and 1968, I found that the species was mainly represented by plants with ligules of about 5 mm. in length, that is, equivalent to Rosser's original S. cambrensis and her subsequent "short" liguled plants. I also noted two other types: one with very short ligules (about 2 - 3.5 mm. in length); and the other completely eligulate (see Plate 7). I did not grow progeny from the very short liguled plants, and thus did not determine if segregation of this ligulate character might have occurred as would have been expected in S. vulgaris var. hibernicus with ligules of this dimension. Progeny of eligulate plants bred true for two generations, and chromosome counts established that these were hexaploid, and hence indubitably S. cambrensis (see Table 36, and Figure 21). These plants only differed from the ligulate forms of the Ffrith S. cambrensis by their lack of ligules, and the associated full expression of androecial development in the peripheral florets of the capitulum. They also possessed smaller achenes (2.4 - 3.0 mm. in length) than those normally present in S. cambrensis (2.8 - 3.5 mm.), but this character was not restricted to the eligulate plants.

A similar eligulate plant was collected by Miss Margaret Gillison from the Wrexham Trading Estate in 1968 (CHR). I determined that, again, the chromosome numbers of its progeny were hexaploid (Table 36), and they bred true for the eligulate character.

It is difficult to postulate the morphological

Plates 7a and 7b Senecio cambrensis:
(both plates are X ½, the background scale being in cm.)

Plate 7a Pictured are three types of S. cambrensis derived directly from material collected at Ffrith. Mean ligule lengths of each plant, from left to right, were: 0, 3.2 mm., and 7.9 mm..

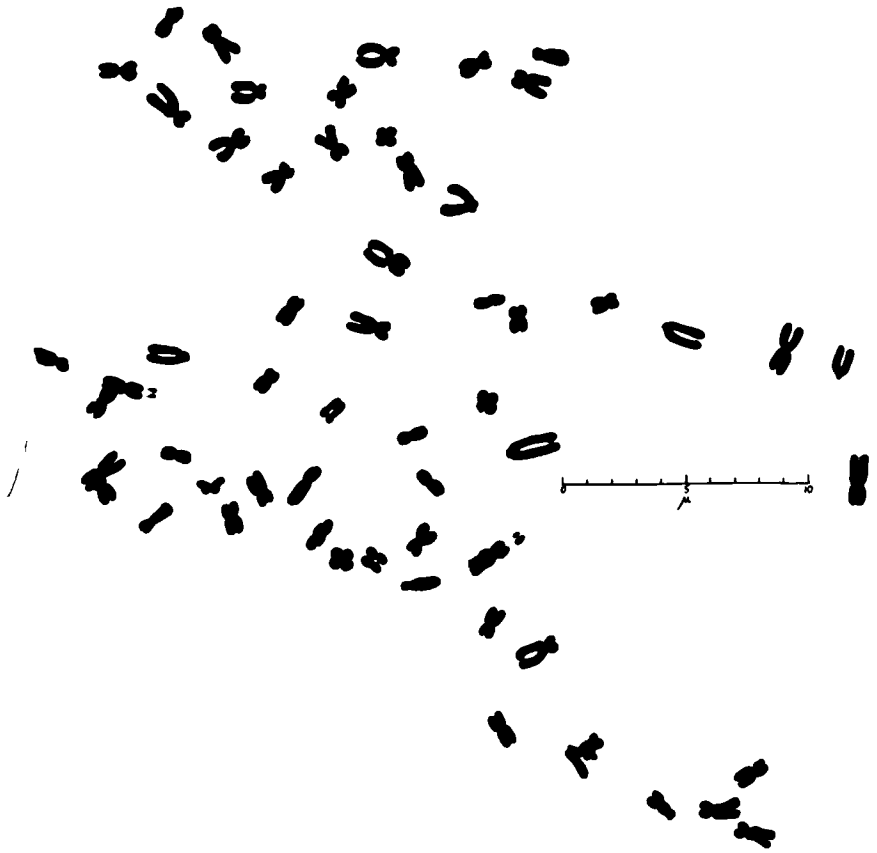
Plate 7b A comparison of a S. cambrensis plant (mean ligule length of 3.2 mm.) and a typical S. vulgaris var. hibernicus plant (mean ligule length 4.8 mm.). Note the slight differences in the appearance of the capitula, and the difference in leaf shape.

Table 36 Chromosome numbers in Senecio cambrensis:

plant code	source of material (see Fig. 19)	2n =	comments
S807:1:1	Ffrith (3)	60	offspring from a ligulate plant
S807:1:2		58	
S807:1:3		60	
S807:1:4		60	
S807:1:5		59	
S807:2:1	Ffrith (3)	60	eligulate offspring from an eligulate plant
S807:2:2		59	
S807:2:5		60	
MG11:1	Wrexham (5)	60	eligulate offspring from an eligulate plant
MG11:2		60	
MG11:3		60	
MG11:4		60	
MG10:2	Wrexham (5)	60	offspring from a ligulate plant
MG10:3		60	
CC1:1	ex Ffrith, hort. Cambridge	60	offspring from ligulate S. cambrensis material maintained at Cambridge Botanic Gardens
CC1:2		60	
CC1:4		60	
CC2:2		60	
CC2:4		59	

characteristics of the ancestral S. cambrensis. The possibility exists, as has already been discussed concerning the S602-type plants (pp. 160-161) that an allohexaploid such as S. cambrensis might not arise simply by the doubling of the genome of an F_1 triploid. Similarly, the possibility that S. cambrensis is of fairly recent origin may mean that the S. vulgaris parent could have been either eligulate or ligulate. Two reasons for this are the common-ness since about 1900 of the ligulate S. vulgaris in the area; and the possibility, already discussed (pp. 157-158) that the introgressed S. vulgaris may hybridise more easily with

Figure 21 Diagram of the chromosomes (2n = 50) of an eligulate plant (S807:2:2, see Table 34) of Senecio cambrensis



S. squalidus.

The close correlation between the classes of ligule length of S. cambrensis and the S602 segregants suggests that a similar interpretation of the genetic system may be applied. In addition, in the Chapter dealing with S. viscosus (pp.197-223) I point out that allohexaploid S. viscosus X S. squalidus possesses ligules quite considerably larger than the F1 triploid, thus indicating the additive nature of the ligule promoting genes. In view of these data, it is probable that the newly formed allohexaploid S. cambrensis

would possess ligules of similar dimensions to S. squalidus (10 - 13 mm. in length) if formed by the doubling of an F_1 triploid genome, especially so if the S. vulgaris parent was ligulate. S. cambrensis of this type has not been recorded. It appears possible, therefore, either that S. cambrensis did not arise by the duplication of the S. X baxteri genome, or that segregation and selection have resulted in a reduction in ligule dimensions.. S. cambrensis, at least in ligule dimensions, may be selectively tending towards the parental S. vulgaris phenotype. It is of relevance to note that all of the progeny grown from field collected seed of the eligulate S. cambrensis plants bred true for the character. Cross pollination with nearby ligulate plants had not occured, and the eligulate taxon, at least, appears to be fairly exclusively inbreeding. These eligulate plants also possess smaller anthers in their disc florets in some cases than do the ligulate strains maintained in botanical collections. A partial continuity between these two extremes was shown by the progeny of the ligulate Ffrith plants, suggesting that the Ffrith S. cambrensis plants share a common gene pool despite their predominantly inbreeding habit.

The similarities between the eligulate S. cambrensis and S. vulgaris are interesting. Selection is apparently favouring characters in S. cambrensis associated with inbreeding, but is this in the cause of increased efficiency of inbreeding; or because of the inherent internal stability of the S. vulgaris genome? There does not appear to have been any segregation of such distinguishing characters as

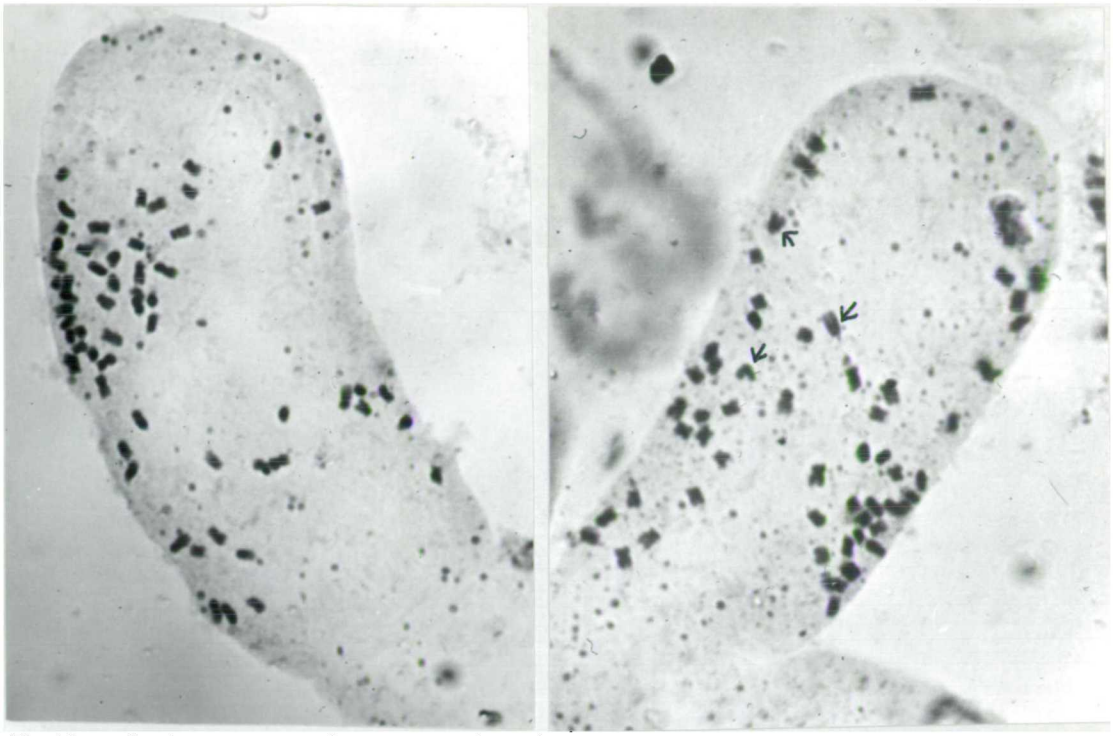
shapes of involucre and leaf, which may suggest the former.

Evolution has progressed in S. cambrensis in at least two other directions than towards parental extremes.

One novel phenotypic character has been found in S. cambrensis. Both parental species in Britain possess marked black tips to their involucral bracts, which are sometimes absent in the outer bracts, but always present in the inner ones. Two S. cambrensis plants, one ligulate (ligules about 5 mm. in length), the other eligulate, were seen near Ffrith by me in 1967, which had no such black tips to the bracts. Whether or not this character was genetically based was not determined, but no such phenotypic variation in the character has been noted in either parent species. In other S. squalidus X S. vulgaris hybrid families the colour--less bract tip character has appeared. In one of the S602 progeny the character was apparent, and the Newbridge-on-Wye family were all of this type. In these tetraploids, at least, the character was genetically determined. The black tipped bract character is absent in some Sicilian S. aetnensis plants, but it is difficult to postulate a continuity of the character from S. aetnensis to S. cambrensis in view of its absence from the British S. squalidus. Presumably the character appears as a result of recombination or loss of genetic material as a consequence of the nature of the tetraploid and hexaploid hybrids.

Plate 8 shows chromosomes with sub-terminal centromeres, up to 8 of which may be present in the somatic complement of S. cambrensis plants. Such chromosomes, as has been

Plate 8 Mitotic chromosomes of Senecio cambrensis:



Both plates are from root tips of the same plant (S807:1:5) derived from Ffrith material. 2n = 59

A shows all 59 chromosomes. Magnification is 1000.

B shows 55 of the 59 chromosomes (4 are out of focus), arrowed are three clearly visible chromosomes with terminal or almost terminal centromeres. In certain cells of this plant six such chromosomes could be counted. Magnification is 1200.

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discussed (see pp. 152-154) are absent in S. squalidus and rare in S. vulgaris. These are probably the results of chromosome re-arrangements following meiotic abnormalities. As a polyploid derived from phylogenetically closely related species, S. cambrensis must have much genetic material duplicated. At least during its early development as a species, therefore, S. cambrensis probably was a subject to

meiotic abnormalities such as multivalent formation, which, as well as leading to chromosome re-arrangements may have led to the selective loss of such genetic material as was in excess of that necessary for the taxon. Selection, however, apparently favours retention of 60 somatic chromosomes. Plants do quite commonly appear with less than that number (see Table 36), but no families have been found with less than that number consistently. It would be interesting to compare the DNA content, by Feulgen cytophotometry, of S. cambrensis with that of the sum of S. squalidus and S. vulgaris in order to ascertain if there has actually been a loss in genetic material. This process of chromosome re-arrangement, with aberrant but viable types being perpetuated by inbreeding may be integral in the "diploidisation" of S. cambrensis into one or more taxa. Such a process, with the evolution of dissimilarities between homeologous chromosomes, was outlined by Darlington (1937).

The occurence of plants with a deficiency of one or more chromosomes (see Table 36) may be the result of chromosome loss during meiosis. The lack of chromosomes supernumary to the 2n = 60 complement probably reflects that unequal segregation, which could result in additional chromosomes in some gametes, is at least a less common phenomenon. Supernumary chromosomes to the hexaploid level do, however, occur in the S. viscosus X S. squalidus hybrids (see Table 43, p.211). Reduced pollen stainability and seed set (see Table 35, and Plate 9) in S. cambrensis are probably a result of genic or chromosomal unbalance. Even so, unless

Table 37 A comparison of the differences between *Senecio vulgaris*, the British *S. squalidus*, and their fertile hybrid *S. cambrensis*:

character		*S. squalidus*	*S. cambrensis*	*S. vulgaris*
2n =		20	(58 -) 60	40
habit		polycarpic	polycarpic	monocarpic
		commonly perennial	commonly perennial	usually annual; coastal ecotypes may be biennial; very rarely perennial
		grows to 40 cm. in cultivation	grows to 50 cm. in cultivation	rarely exceeds 30 cm. in cultivation
		branching lax and widely spreading; side shoots common at base of stem	intermediate branching; side shoots common at base of stem	branching close and usually restricted to upper parts of stem; basal shoots very rare
middle cauline leaves (see Fig.)	lobes	oblong, leaves sometimes bipinnatifid	oblong, irregularly pinnatifid	oblong, to triangular, to semi-circular
	margins	irregularly dentate to bidentate	irregularly dentate to lobulate	regularly to irregularly dentate to bidentate
	auricles	variable in size, but usually small	small	variable in size, occasionally large
	outline	oblong	rhomboid	oblong to spathulate to rhomboid
capitula	arrangement	loosely or singly on upright stalks	in tight clusters at first, becoming more lax with development	usually in tight clusters, erect or drooping
	shape	large, bell shaped	intermediate	small, cylindrical

- continued -

ligules	number	usually 13	0; 8 - 13 (- 15)	0; 7 - 13
	length	9.2 - 13.2 mm.	0; about 2.0 - 8.0 mm.	0; 1.0 - 5.3
	breadth	2.0 - 4.2 mm.	0; about 1.5 - 2.5 mm.	0; about 1.0 - 2.0 mm.
	colour	orange yellow	intermediate	pale to medium yellow
involucral bracts	length of outer	¼ length of inner	variable, ¼ to ½ length of inner	¼ - ½ length of inner
	colour of tips	black	black to colourless	black
achenes	length	2.0 - 2.6 mm.	2.4 - 3.5 mm.	1.8 - 2.4 mm.
	hairs	medium, in grooves	medium to long, in grooves	medium, in grooves
pollen	production	copious	limited in some races, copious in others	very limited in most races, fairly copious in others
	diameters	22.1 - 27.4 μ	29.8 - 33.2 μ	22.2 - 27.2 μ
	stainability	(91.2 -) 98.3 - 100.0%	65.1 - 96.1%	(82.3 -) 94.8 - 100.0%
	pore number	3	3 - 4	3
breeding system		self-incompatible and outbreeding	self-compatible and predominantly inbreeding	self-compatible and predominantly inbreeding
seed set		0 - 100% depending on degree of cross-pollination	15 - 70%	usually near to 100%
mildew susceptibility		slight	slight	depending on race: slight to extreme
distribution		widespread and common in England, Wales and Ireland (also in South Italy)	locally common in a few stations in North Wales and Cheshire	widespread and often very common throughout Eurasia

Notes on Table 37 :

Characters are for plants grown under favourable natural or cultivated conditions. Under adverse conditions (such as in coastal or dry cinder areas) plant growth may be suppressed to the extent that only solitary capitula are produced, and floral part numbers may be reduced.

In other diagnostic characters, including achene colour, trichome characteristics, habitat, ligule reflexion, disease susceptibility, and flowering period all three species are essentially the same.

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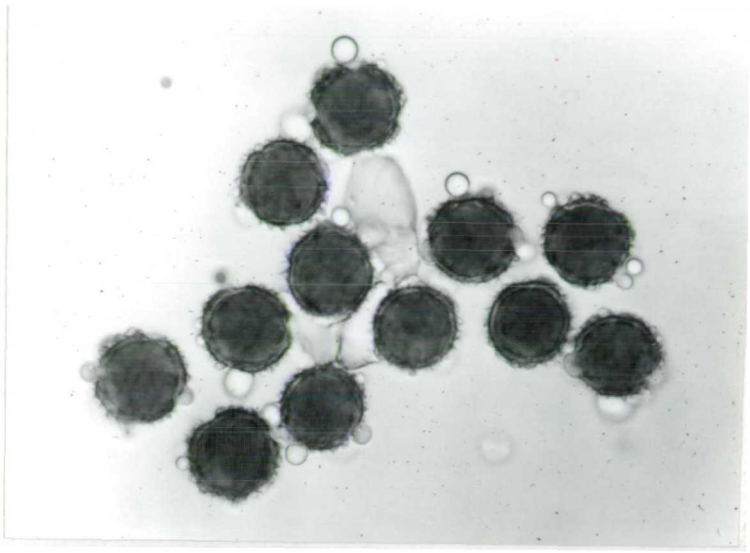
the germ cell lines differ from the purely somatic tissues, it is probable that selection against chromosome deletions in gametes operates at the functional gametophyte level rather than on pollen viability. This would explain the general maintainance of the 2n = 60 chromosome number despite the high stainability of pollen produced by plants with 2n = 58 or 59.

Pollen mother cell meiosis is difficult to study in S. cambrensis, but on good preparations it is apparent that there are less than the 30 metaphase chromosome associations that would represent purely bivalent formation. Usually about 27 - 28 associations are apparent, and the fair regularity of the subsequent meiotic division indicates that these are probably bivalents and quadrivalents, with two or three of the latter being present.

Several natural allopolyploids are known which retain a slightly irregular meiosis as an apparent consequence of their origins (Riley, 1960). They include Brassica juncea, Nicotiana tabacum, Poa annua, and Gossypium barbadense.

Plate 9 Pollen of Senecio cambrensis:

X 400



The plate shows pollen of a derivative of the Senecio cambrensis maintained at the Cambridge Botanic Gardens. The pollen is predominantly 4 pored; is highly fertile (89.3% stained of 493 grains counted); and has a mean pollen diameter of 31.4μ, 2 X S.E. of 1.9μ (50 grains were measured).

Such situations, where the process of diploidisation is incomplete, must mean that homeologous chromosomes or chromosome segments capable of pairing are retained in the population. Of course, such pairing may still result in a regular meiosis by the formation of particular quadrivalent configurations (McCollum, 1958), or selection may favour certain genetic constituents to the extent that associated infertility is tolerated. Alternatively, the retention in the population of chromosomes capable of allosyndetic pairing may be due to a breeding system which encourages both the retention of particular chromosome types in the population (that is, inbreeding) and the recombination of these different

chromosome types (outbreeding). Therefore, Brassica juncea and the other species mentioned above may owe their incomplete diploidisation to being predominantly inbreeding, but also participating considerably in a larger gene pool. It will be interesting to see how S. cambrensis (if it survives at all) will progress. At present it appears to be in the same situation as B. juncea, where both in- and outbreeding occur, with the associated meiotic irregularities and slight infertility. It appears that new karyotypes and phenotypes are becoming established as a consequence of inbreeding. Subsequent evolution of S. cambrensis may well depend upon the evolution of its breeding system. Retention of any significant degree of outbreeding may mean that a single taxon is maintained; inbreeding may result in the separation of different taxa due to the accumulation of chromosomal differences between races and the resultant hybrid sterility (Stebbins, 1957).

Despite its tendency to segregate, S. cambrensis remains a recognisable taxon, and is easily distinguished from both parental species. Theoretically, S. cambrensis may segregate further, and S. vulgaris may become more introgressed with S. squalidus genes until difficulty is encountered separating the two taxa on morphological grounds. These considerations do not apply to the present situation. New allohexaploid families of S. cambrensis may arise by re-hybridisation of the parental species, but it remains to be seen if these will be morphologically or genetically continuous with the present taxon. The only morphological continuity between

S. cambrensis and any other species is supplied by the nothomorphic families resembling S602 (that is, segregating, tetraploid progeny of S. squalidus X S. vulgaris). The S602 - type families are not, in themselves, of classificatory importance, and so the isolation of S. cambrensis justifies its retention as a species. A revised description of S. cambrensis compared with its parental species is given in Table 35.

Only the ligulate character is sufficiently distinctive to permit taxonomic distinction below the species level in S. cambrensis. Of the ligule length classes in S. cambrensis I suggest that the very short (2 - 3.5 mm.) ligule length plants are probably of a non-permanent type, subject to segregation; the other ligulate types (5 - 8 mm. in length) are not sufficiently distinct to merit division; and the eligulate form should be recognised as forma eligulatus. As such, a similar taxonomic treatment is applied to a biological situation which is similar to that in the ligulate S. vulgaris.

SENECIO X LONDINENSIS

Lousley (1946) first described the hybrid between Senecio squalidus and S. viscosus as S. X londinensis from several plants which had been found on bombed wastes in London, where the two parental species had become very plentiful. Besides several London stations, Lousley (loc. cit.) also reported the hybrid from Ham gravel pits in Surrey; and from a railway siding at St. Mary Cray, west Kent.

The hybrid is easily recognisable both in the field and in the herbarium, and a comparison between it and the parental species is given in Table 38 (see also Plates 10 and 13; and Figure 23). It is morphologically consistent, and up until the present, no report has been made of seed set in the hybrid. Herbarium specimens of the hybrid that I have seen are given in Appendix Table 15.

My investigations of S. X londinensis commenced in July, 1967, when, following a report of P.M. Benoit (personal communication), I observed six individual hybrid plants from an extensive mixed population of S. squalidus and S. viscosus on railway shingles and cinders at Barmouth Junction, Merionethshire. These hybrids were all given the code number of S823. Also present at Barmouth were eligulate and ligulate S. vulgaris, and the normal ligulate S. jacobaea, but no anomalous plants of these species were seen.

One of these six hybrids (designated S823(8r)) was unlike the others. S823(8r) was of weak growth, consisting

Table 38 The characteristics of Senecio squalidus, S. viscosus, and S. X londinensis:

character		S. squalidus	S. X londinensis	S. viscosus
2n =		20	30	40
habit		polycarpic	polycarpic	monocarpic
branching		lax and widely spreading	irregular and widely spreading	fairly regular
trichomes:	glands	very sparse	dense	very dense
	clubs	sparse	sparse	usually absent, see Table
	whips	sparse	sparse	
leaf outline		intermediate (see Figure 23)		
ligules:	number	usually 13	(7 -) 13	8 - 13
	length	9.2 - 13.2 mm.	6.4 - 9.1 mm.	4.6 - 6.1 mm.
	breadth	2.0 - 4.2 mm.	1.2 - 2.1 mm.	1.0 - 1.5 mm.
	colour	orange yellow	greenish yellow	greenish yellow
	curvature	reflexing	strongly reflexing	strongly reflexing
involucral bracts: length of outer		< ¼ length of inner	variable	ca. ½ length of inner
tip colour		black	black	brown or green
capitulum shape		bell shaped	intermediate	conical
fertile achenes:	length	2.0 - 2.6 mm.	1.4 - 3.5 mm., often mis-shapen	2.7 - 4.2 mm.
	hairs	in grooves	short, in grooves	glabrous
	colour	light to dark brown or green	light to dark brown	yellow to dark brown
flowering period (calendar months)		(1 -) 3 - 11 (- 12)	5 - 11	(4 -) 5 - 10 (- 11)

Note: Measurements given for achenes and ligules are means based on a minimum of 10 from individual plants grown in cultivation. Plants under natural conditions may exhibit slight reductions in these dimensions.

Although this gives the range of flowering periods recorded in each taxon under conditions of cultivation, the plants at Barmouth (see text) were noteworthy in that in July, 1967, S. squalidus was well into seed, S. X londinensis was in flower, and S. viscosus was in a pre-flowering stage. This may be another intermediate character of the hybrid.

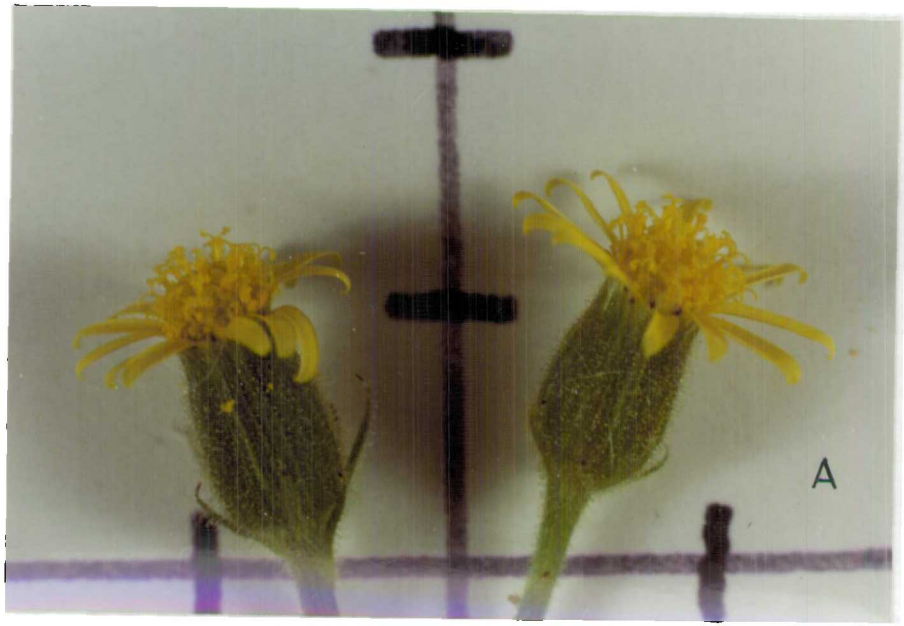


Plate 10 Capitula of Senecio squalidus, S. viscosus, and their F_1 triploid hybrid S. X londinensis:

A = S. viscosus (S3:1:1)
B = S. squalidus (S807:1:2:4)
C = S. X londinensis (Spont. 1)

The plates are X 3.3; the background scale being in cm.

only of a single upright stem with few, small leaves. This is in contrast to the normal growth form of the hybrid (see Plate 13), which is vigorous and much branched. S823(8r) was also less glandular than the other hybrids. It had smaller, relatively longer capitula, with the ligules being paler yellow, smaller, and relatively narrower than the normal hybrid. The number of ligules on this plant in the field was 8 per capitulum, whereas the normal hybrid had 13. In cultivation, however, both types showed some variation, so that S823(8r) occasionally showed up to 11 ligules, and the normal hybrids (including ones from other sources) sometimes produced capitula with as few as 7 ligules.

The hybrid plants were propagated by cuttings, and 5 and 10 plants were produced, respectively, from S823(8r) and one of the normal Barmouth hybrids, which was designated S823(13r).

Both S823(8r) and S823(13r) were found to possess the expected triploid chromosome number of 2n = 30. At P.M.C. meiosis S823(13r), in common with subsequently investigated F_1 S. X londinensis showed univalents and bivalents, ranging from 6I + 12II to 10I + 10II. Very rarely were associations greater than bivalents met with in these F_1 hybrids, and multivalents involving more than three chromosomes were never positively identified. In contrast, S823(8r) showed a high number of multivalents, and considerable bridge and fragment formation.

Both S823(8r), and F_1 hybrids such as S823(13r) were

highly pollen sterile (see Table 39 and Plate 11): such stained pollen as was found usually being large and with more than the normal three apertures per grain. Other abnormalities, such as mis-shaped and siamesed grains were also observed.

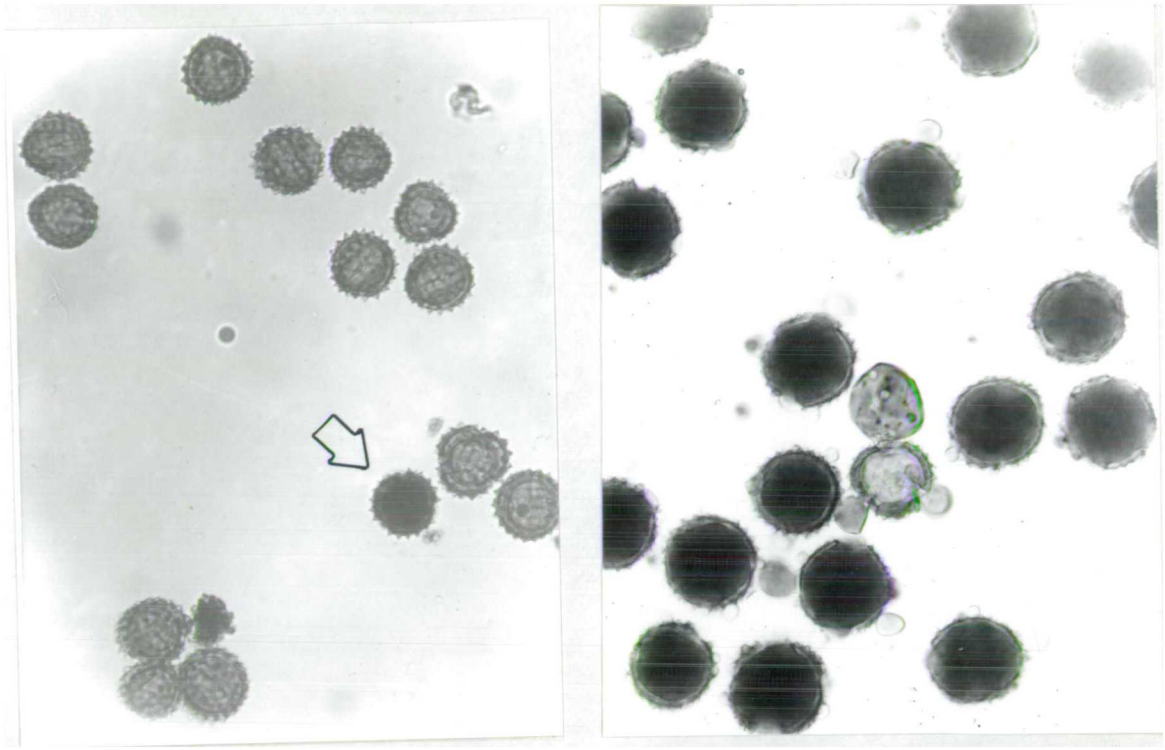
Seed set in both cases was extremely low, and in all cases never exceeded about one seed set in two or three heads (about 0.4% as a maximum, - see Table 40). It was far more common for 40 - 50 heads to be examined before a single seed was found. Attempts to pollinate both types with the parental species failed to set seed. This indicates that the hybrid pollen fertility, despite being very low (about 5% are stainable) is probably not limiting on seed set, and that ovule or embryo inviability are more probably responsible. That embryo death may occur is perhaps indicated by the fairly frequent growth of seeds to about twice the length of the normal unset seeds, before dying. These long, unset seeds attained a length of about 3 mm., and probably occurred at a frequency of about 5 - 10%, although I made no definite counts of their occurrence.

The triploid chromosome number indicates fairly conclusively that the diploid S. squalidus was involved in the origin of S823(8r). The glandulosity of S823(8r) also indicates a parentage in S. viscosus or S. sylvaticus, or even S. X viscidulus (as in the S203 X S. squalidus hybrid described on p. 226). At the Barmouth locality, however, there was no sign of S. sylvaticus, or of S. X viscidulus. It appears to be most probable that S823(8r)

Table 39 Pollen stainability and diameters in Senècio X londinensis and its progeny, - numbers of grains counted or measured are given in brackets:

plant code number, generation, etc.	2n =	% stained	diameter in μ			comments
			mean	s.d.	range	
F1 triploid hybrid						
S823(13r)	30	3.9 (257)	35.89	3.82	29.76 - 41.85 (27)	
		4.8 (658)	40.69	2.60	34.41 - 43.71 (12)	
		5.2 (248)	34.34	2.34	30.69 - 39.06 (13)	
Spont.1	30	8.0 (50)	38.36	5.94	29.76 - 42.78 (4)	
CS7(3x)	30	7.1 (308)	31.04	1.80	27.90 - 34.41 (13)	- moribund grains only
			34.06	2.20	33.48 - 39.06 (8)	- fully stained grains
MEAN		5.5 (1521)	35.50	1.02	27.90 - 43.71 (77)	
F1 hexaploid hybrid						
CS18	60	77.0 (435)	32.16	1.91	27.90 - 36.27 (50)	
CS1	60	67.5 (326)	31.94	2.32	26.04 - 39.06 (50)	
		72.0 (457)	32.02	1.86	26.04 - 34.41 (50)	
S823(13r)Col.1	60	83.7 (294)	33.63	2.05	26.97 - 39.06 (50)	
CS7(6x)	(60)	71.1 (329)	31.69	1.79	26.97 - 36.27 (50)	- mixoploid: 2n = 59 - 61
MEAN		74.6 (1841)	32.29	0.76	26.04 - 39.06 (250)	
F2 triploid from F1 triploid						
S823(8r)	30	2.5 (367)	32.86	4.01	26.04 - 44.64 (21)	
		2.4 (473)	35.54	3.12	25.11 - 39.06 (14)	
S823(13r)L1	30	1.6 (193)	34.92	3.43	25.11 - 42.78 (16)	
F2 pentaploid from F1 hexaploid						
S823(13r)Col.10:4	49	1.8 (500)	34.78	2.28	32.55 - 39.99 (10)	
F2 pentaploid from F1 triploid						
S823(13r)L3	48	1.7 (518)	32.20	1.69	29.76 - 34.41 (8)	
F3 pentaploid from F2 triploid						
S823(8r):1	48	9.2 (543)	39.08	3.80	31.62 - 45.57 (35)	
S823(13r)L1:1	48	5.8 (312)	35.34	2.92	25.11 - 39.06 (20)	
F4 tetraploid from F3 pentaploid						
S823(13r)L1:1:1	44	14.9 (327)	33.29	1.93	26.04 - 36.27 (50)	
S823(13r)L1:1:2	43	19.1 (435)	32.63	2.41	25.11 - 36.27 (50)	
S823(13r)L1:1:3	43	-	33.64	1.87	26.04 - 37.20 (50)	
S823(13r)L1:1:4	44	21.1 (294)	35.28	2.02	27.90 - 39.06 (50)	
	AN	18.4 (1056)	33.71	1.80	25.11 - 39.06 (200)	

Plate 11 Pollen of the hybrid Senecio.X londinensis (= S. viscosus X S. squalidus), stained in cotton blue in lacto-phenol:



A B

A = the F_1 triploid hybrid. Arrowed is one of the rare stained pollen grains. The specimen is S823(13r), see Table 39.

B = the F_1C_0 hexaploid (derived by colchicine treatment of a triploid similar to S823(13r)). The specimen is CS18, - see Table 39.

Both plates are X 410.

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is one of the very rare offspring of an F_1 S. X londinensis plant. This is supported by the subsequent production of triploid plants from S823(13r). S823(8r) was, therefore, assumed to be a natural F_2 triploid S. X londinensis, although the possibility exists that it may have been of an even later generation from the original species hybrid.

Table 40

Comparison of pollen, achenes, and ligules in triploid and hexaploid F_1 *Senecio X londinensis*, and in the hexaploid progeny of the hexaploid F_1.

Bracketed figures refer to the number of plants from which measurements were taken. Numbers of individual measurements per plant were: pollen diameter 4 - 50; pollen stainability 50 - 658; achene length 4 - 53; achene set 137 - 2821; and ligule length 10 - 20.

		F_1		F_2
		triploid	hexaploid	hexaploid
POLLEN DIAMETER (in u)	mean	35.50 (3)	32.29 (4)	†31.93 (1)
	s.d.	1.02	0.74	1.76
	range	27.90 - 43.71	26.04 - 39.06	26.04 - 36.27
POLLEN STAINABILITY (%)	mean	5.5 (3)	74.6 (4)	†69.3 (1)
	range	3.9 - 8.0	67.5 - 83.7	
ACHENE LENGTH (in mm.)	mean	2.84 (1)	3.72 (8)	†
	s.d.	0.12	0.31	
	range	2.6 - 3.1	2.9 - 4.6	
ACHENE SET (%)	range	0.0*- 0.4 (10)	0.0 - 18.6 (8)	†6.2 (1)
LIGULE LENGTH (in mm.)	range	6.4 - 9.1 (10)	8.5 - 9.5 (8)	10.5 - 13.5 (30 - 40)

* seed set was so low in most of the F_1 triploids that it was not assessed beyond searching many capitula for set seeds.

† besides the measurements given here, the other 30 - 40 F_2 hexaploids grown visually resembled the F_1 hexaploids.

S. X londinensis plants were also produced by pollinating S. squalidus with S. viscosus, a total of 40 hybrids being very easily produced by this method. Twenty of these hybrids were tested, and all had the expected chromosome number of 2n = 30. Some of these hybrids were rendered poly--ploid by the application of colchicine, either at the cotyledonary stage, or on axillary buds of more mature plants. Cuttings from S823(13r) were similarly treated in their axils. Rooted cuttings taken from these treated plants (the C_0 generation) when in an advanced stage of growth, showed by chromosome counts whether the treatment had been successful (2n = 60), or unsuccessful (2n = 30). In two cases consistent counts slightly below the hexaploid (2n = 60) level were encountered, one of 2n = 58, the other of 2n = 59; and in one case a plant had chromosome numbers in different cells ranging from 2n = 59 to 61.

These allohexaploid C_0 plants were morphologically uniform, and were very similar to the F_1 triploids except for slight increases in sizes of capitula, ligules, and achenes (see Tables 40 and 41). There was, however, a great increase in pollen stainability and seed set (see Plate 11, and Tables 39 and 42).

The progeny from F_1 triploids and F_1C_0 hexaploids showed two very interesting features. Certain characteristics of the hexaploid only became fully expressed in the C_1 generation, - a feature also shown by autotetraploid S. squalidus (see pp. 146 - 148), and which is summarised in Table 31 (p.147).

Table 41 Achene lengths (in mm.) of the triploid F_1 and the F_1C_0 hexaploid Senecio X londinensis:

plant	2n =	no. seeds measured	mean	s.d.	range
TRIPLOID					
S823(13r)	30	30	2.84	0.12	2.6 - 3.1
HEXAPLOID					
S823(13r)	60	27	3.73	0.16	3.4 - 4.0
CS1	60	30	3.70	0.34	2.9 - 4.2
CS7	(60)	38	3.48	0.25	3.0 - 3.9
CS18	60	53	3.77	0.25	3.3 - 4.2
CS25	60	14	4.18	0.31	3.6 - 4.6
CS26	58	11	3.66	0.23	3.3 - 4.1
CS27	59	6	3.75	0.33	3.4 - 4.2
CS28	60	4	3.73	0.44	3.3 - 4.3
total		183	3.72	0.31	2.9 - 4.6

Note: The chromosome number of CS7 in individual root tip cells ranged from 59 to 61.

The results for the triploid are derived from a great number of inspected capitula from several plants obtained by taking cuttings from a single plant - S823(13r). Hexaploids resulting from colchicine treatment of certain of these cuttings are grouped together as the hexaploid S823(13r). The other hexaploids are derived from plants unrelated to these.

The vigour of the offspring of the C_0 hexaploids is shown in Plate 12.

In addition, three classes of offspring were being produced by the triploid and hexaploid F_1 plants with regard to chromosome numbers. The triploids produced plants with chromosome numbers at or around the triploid, pentaploid, and hexaploid levels (some of these are shown in Plate 14); and the hexaploids produced plants at about the pentaploid and hexaploid levels. These results are summarised in Table 43. Reference to Table 31 (p.147) shows another feature of

Table 42 Seed set in the triploid F_1 and the hexaploid F_1C_0 Senecio X londinensis

plant	2n =	seeds counted: set	unset	total	% set	range of seed set per head	no. of heads	mean no. of seeds per head
TRIPLOID								
S823(13r)	30	40	2084	2124	1.6*	0 - 1	40	50.5
		0	-	-	-	-	136	-
MEAN		40		ca. 8888	ca. 0.4	0 - 1	176	
HEXAPLOID								
S823(13r)	60	46	421	467	9.9	4 - 14	7	66.7
CS1	60	69	303	372	18.6	1 - 21	6	79.0
CS7	(60)	20	654	674	3.0	0 - 3	11	61.3
CS18	60	131	725	856	15.3	2 - 39	11	77.8
CS25	60	7	130	137	5.1	3 - 4	2	68.5
CS26	58	2	215	217	0.9*	0 - 1	3	72.3
		14	-	-	-	-	39	-
CS27	59	5	2816	2821	0.2	-	51	55.3
CS28	60	1	-	-	ca. 0.1	0 - 1	28	-
MEAN (omitting CS28)		294		ca. 6364	ca. 4.6	0 - 39	130	

Notes: Seed set in other triploids was of the same order as S823(13r).

The chromosome number of CS7 in individual root tip cells ranged from 59 to 61.

An asterix (*) indicates that the % seed set has been estimated using the mean number of seeds per head only from those which were counted.

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the offspring of the hexaploid plants, namely that in all cases except the offspring of CS7 they fell into two morphological classes corresponding to their approximate ploidy. This indicates that specific chromosomes were involved at each ploidy level, and the adherence of chromosome numbers to ploidy levels indicates that segregation and recombination of whole

Plate 12 The hexaploid F_1 Senecio X londinensis and the progeny of such hexaploids:
(The background scale in all cases is in cm.)

A = the F_1C_0 hybrid X 0.16 (CS25, 2n = 60)
B = a hexaploid C_1 X 0.12 (CS18:2, 2n = 59)
C = a pentaploid C_1 X 0.11 (S823(13r)Col.10:6, 2n = 50)

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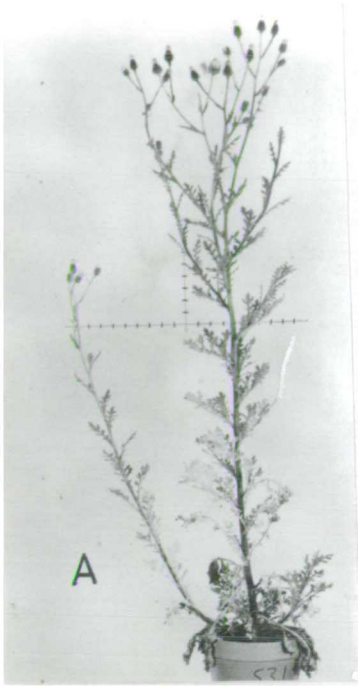
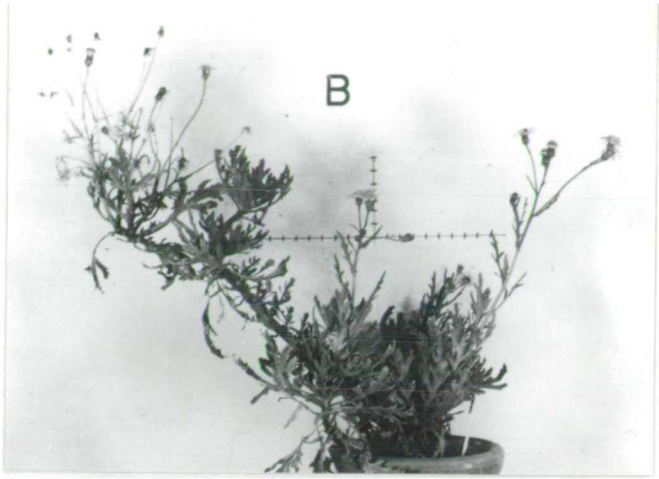
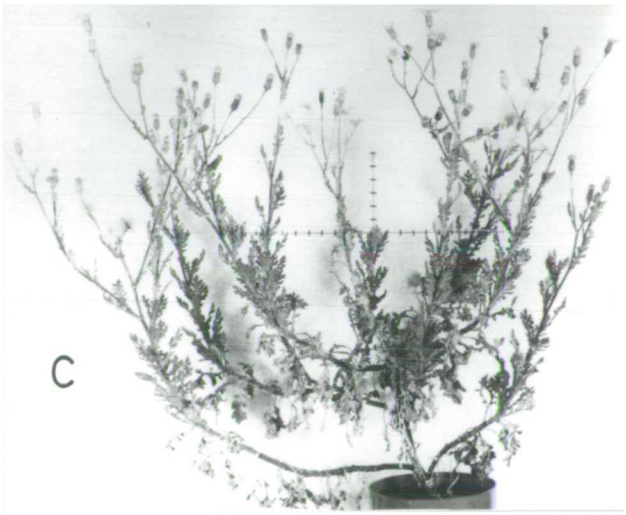
genomes supplied the viable offspring of the hexaploids. In the F_1 triploid the production of approximately 10 bivalents and 10 univalents will result in gametes with 10 - 20 chromosomes; and non-reduction will result in gametes with 30 chromosomes. The production of offspring with chromosome numbers of about 30, 50, and 60 indicates both that non-reduction has been taking place; and that preferential segregation of the univalents, or selection at a stage subsequent to gamete production in favour of gametes with

Plate 13 Senecio squalidus, S. viscosus, their F_1 hybrid (S. X londinensis), and the F_4 derivatives of this hybrid: (in all cases the background scale is in cm.)







A = S. viscosus X 0.16 (S3:1:2, 2n = 40)

B = S. squalidus X 0.17 (S31:4, 2n = 20)

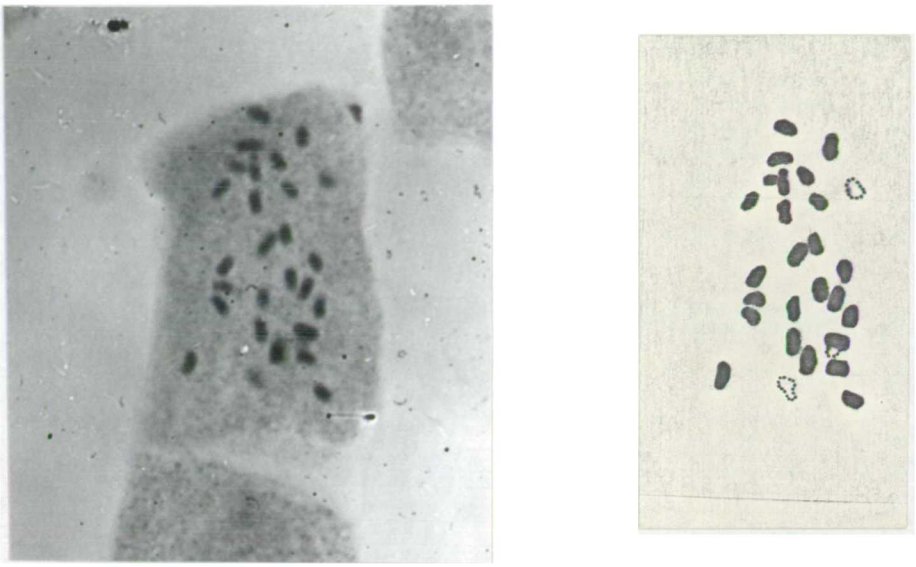
C = S. X londinensis X 0.17 (S823(13r), 2n = 30)

D and E = F_4 derivatives from S. X londinensis:

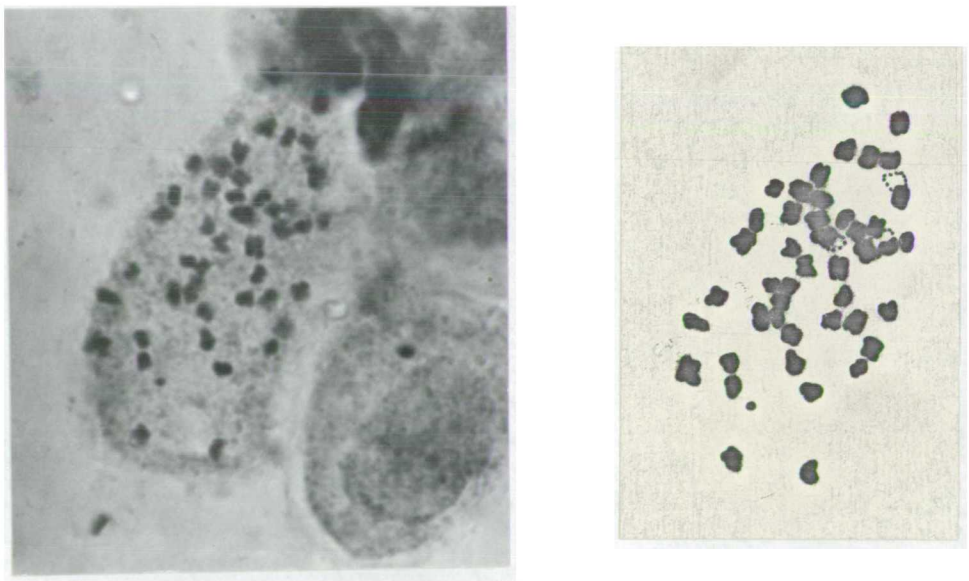
D = S823(13r)L1:1:1 X 0.17 (2n = 44)

E = S823(13r)L1:1:2 X 0.17 (2n = 43)

Plate 14 Mitosis in the progeny of a triploid (2n = 30) Senecio X londinensis:



S823(13r)L2 2n = 30



S823(13r)L3 2n = 48

Photographs are taken from squashed root tips stained in Feulgen. Chromosomes out of focus are indicated in the explanatory diagrams by dotted outlines.

Both photographs are X 1000.

Table 43

Chromosome numbers of Senecio squalidus (2n = 20) X S. viscosus (2n = 40) and its progeny:

PARENT: type	specimen code no.	2n =	CHROMOSOME NUMBERS OF PROGENY: 3x 29	30	31~43	44	45	46	47	48	49	5x 50	51	52	53	54	55	56	57	58	59	6x 60	61
F_1 3x	C.S.1	30			~				1	1	2 (1)	4 (1)											
	S823(13r)	30		2	~					1								1					
F_1 colchi-6x	C.S.18	60			~						2	2* 1 (1)	1	1				1	(2)	2	3	2 (1)	1 (1)
	C.S.7	60*			~						1	1* 1		1	1					1	1	3	
	S823(13r) Col.10	60			~					2 1*	1*	2* 3								(1)			
	S823(13r) Col.7	60			~										1				1	1			
F_2 3x	S823(13r): L1	30			~					1													
	S823(8r)	30			~					3													
F_3 5x	S823(13r): L1:1	48			~	2	2																
TOTAL:				2	~	2	2		1	9	7	16	1	2	2			2	3	5	4	6	2

Note: Bracketed figures refer to approximate counts; An asterix (*) refers to the count being the approximate mean in a mixoploid tissue; In both cases counts are within ±2.

haploid, diploid, or triploid complements of chromosomes resulted in the production of gametes with about 10, 20, or 30 chromosomes. Thus, gametes with 10 and 20 chromosomes can combine to give a 2n = 30 offspring, and so on. That the 2n = 30 F_2 plants (such as S823(8r)) are produced in such a manner rather than parthenogenetically is indicated both by their rarity and by the quite considerable morphological differences both between themselves and with their parent F_1. Similarly, it appears that the hexaploids produce offspring by the fusion of 20 and 30 chromosome gametes to give 50 and 60 chromosome offspring. Fig.22 shows such a pentaploid complement.

The possibility exists that diploid and tetraploid progeny could have been produced by the triploids, and tetraploids by the hexaploids, by fusion of the appropriate gametes. Offspring of this type were not observed, but their implications are discussed later.

The progenies of the hexaploid C_0 plants were not studied in detail further than the self-produced C_1 generation. A few C_2 plants from hexaploid C_1 parents were raised, however, and were morphologically indistinguishable from their parents. This showed that the newly formed allohexaploid was not markedly segregating.

The further progenies of certain of the triploids were studied in some detail, one series through to the F_4 generation, and are discussed below.

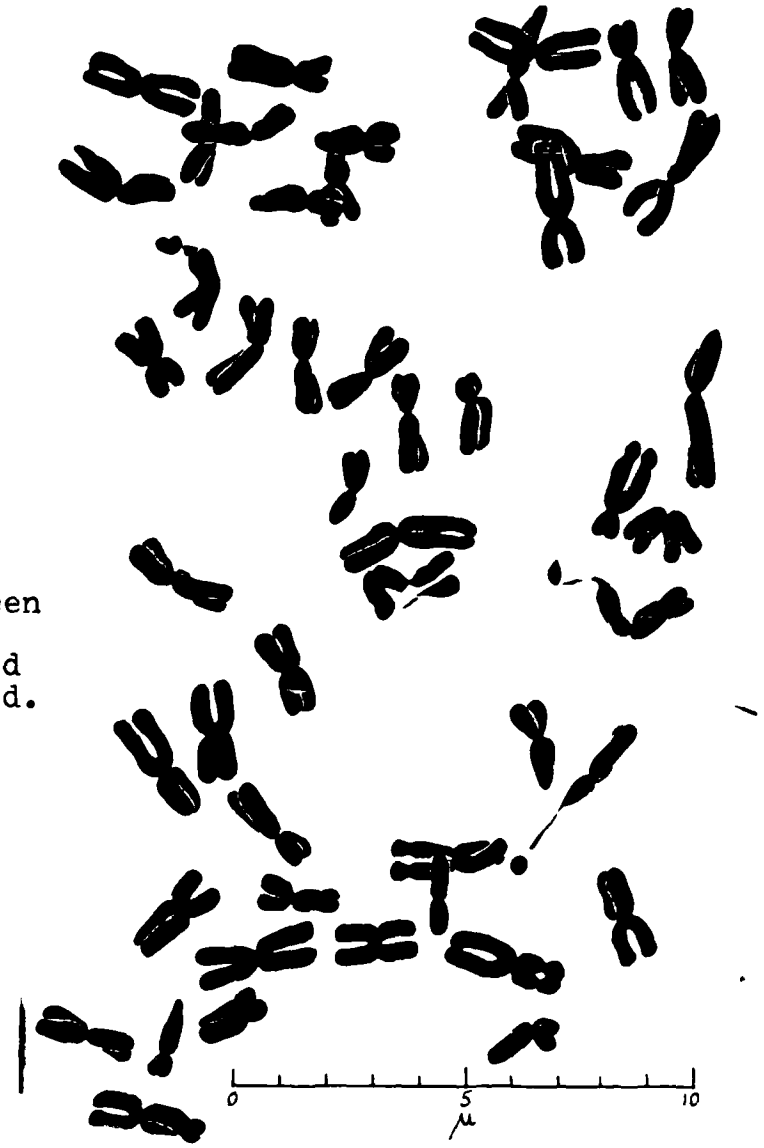
Seed set in all pentaploids and in all triploids was very low, never exceeding about 0.5%, even under conditions of

Figure 22 A camera lucida drawing of the chromosomes of the pentaploid progeny of an allohexaploid C_0 S. X londinensis.

The specimen is S823(13r) Col. 10:3, the root tips of which were mixoploids with 2n = 48 to 50.

In this cell 2n = 49

Note the number of satellited chromosomes: in this tissue (and typically in others of its kind) between 5 and 7 satellites could be distinguished.



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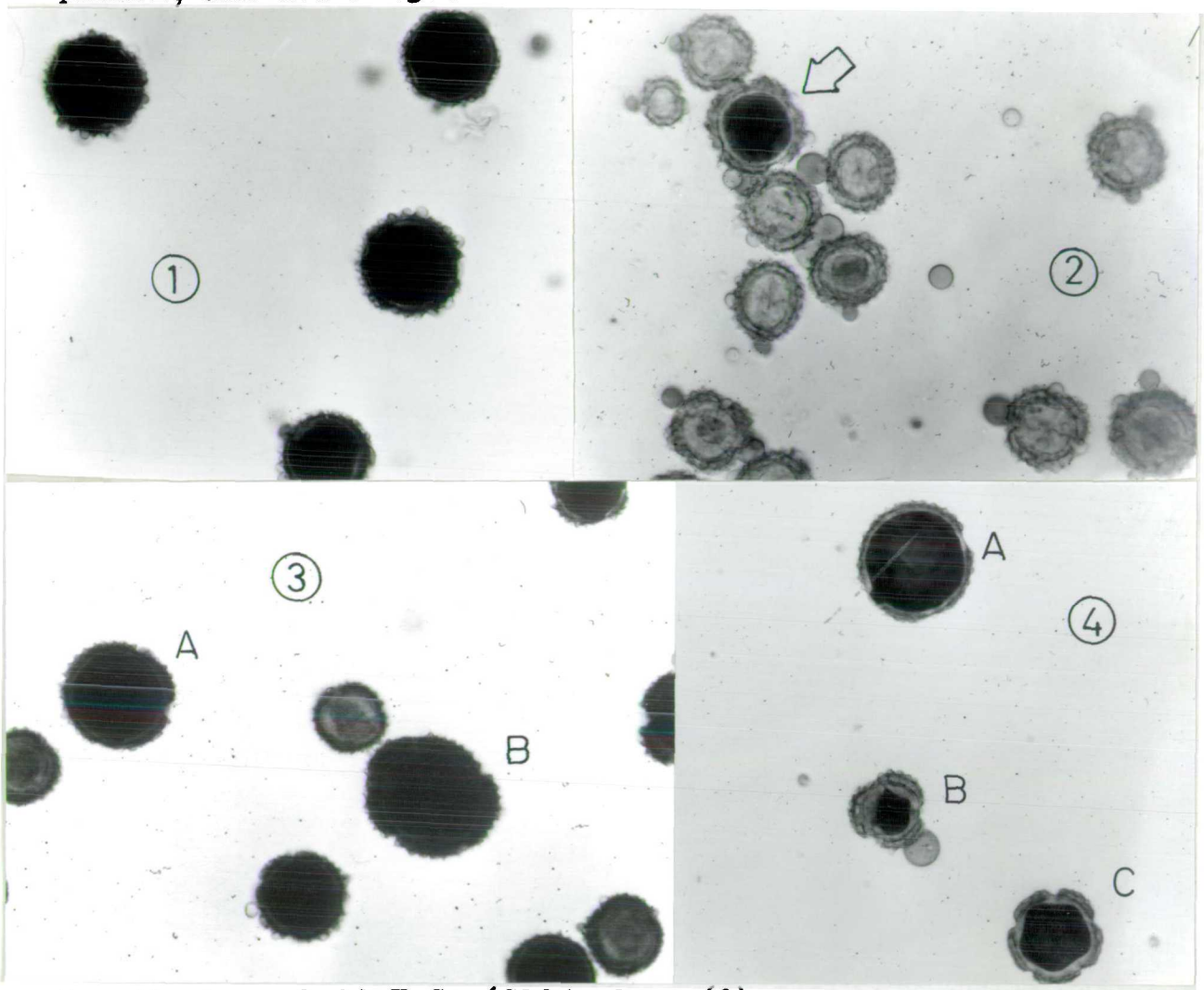
open pollination. Pollen stainability was occasionally high, but grains were usually morphologically abnormal (see Plate 15). Pollen mother cell meiosis in a pentaploid is shown in Plate 16. A total of 14 offspring from triploid F_1 S. X londinensis were examined cytologically (see Table 41),

Plate 15 Pollen of various pentaploids derived from Senecio X londinensis. Included for comparison is the pollen of a hexaploid. All are stained in cotton blue in lacto-phenol, and are X 430:



1 = the hexaploid F_1C_0 (CS25, 2n = 60).

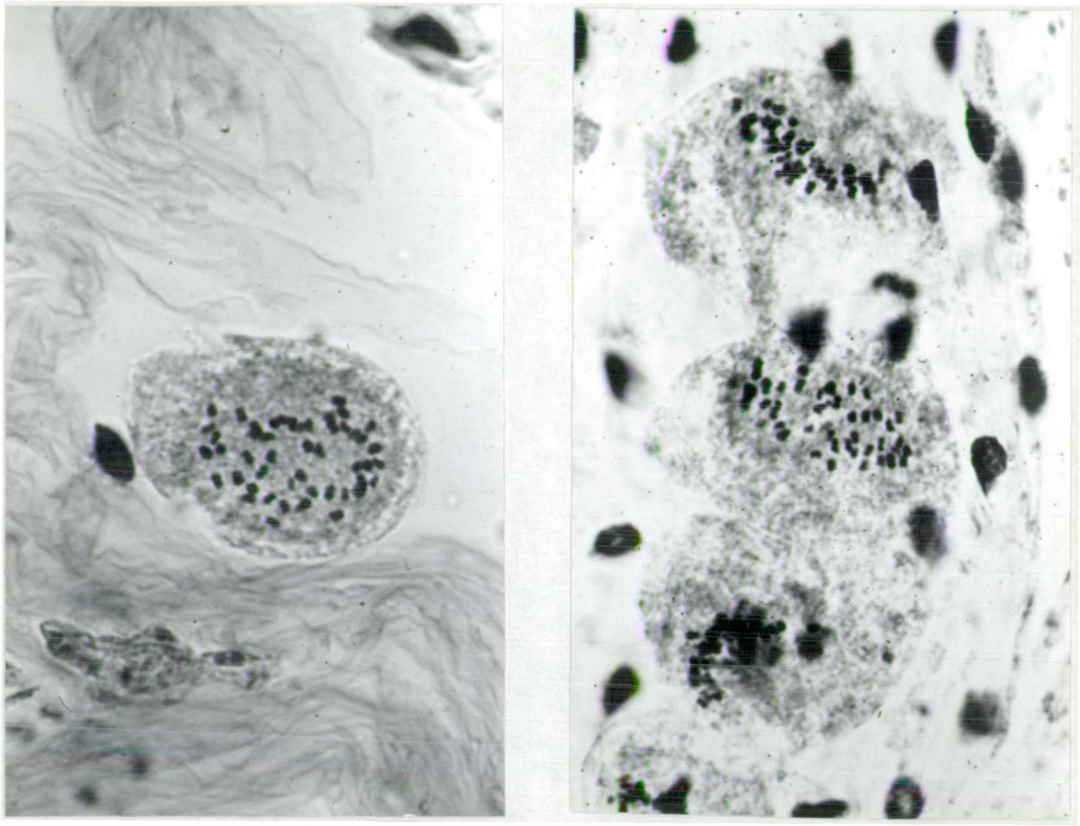
2 and 3 are C_1 pentaploid derivatives of F_1C_0 hexaploids:
2 = S823(13r)Col.10:4 (2n = 49). The stained grain (arrowed) lacks pollen tube primordia.
3 = CS7:6 (2n = 52). Pollen stainability was atypically high in this plant (29.4% of 394 grains), and very high pollen tube primordia numbers and abnormally large grains were observed. Pollen grain A had 6 primordia; pollen grain B had in excess of 10 primordia, and measured about 43μ across its least diameter.

4 = a pentaploid derived from an F_2 triploid (S823(8r):1, 2n = 48). Pollen grains C and B are stained but moribund, A has pollen tube primordia. A has 4 pores, B has 3 (the normal parental species number), and C has 5.

and fell into the three groups already mentioned: - triploid (2 plants); more or less pentaploid (11); and nearly hexaploid (1). The triploid progeny of one F_1 triploid (S823(13r)) was designated S823(13r)L1. This had a very low seed set, of the order of its parent, but produced one large vigorous plant with 2n = 48 (S823(13r)L1:1) which set seed at a rate of 1.2% (32 seed set from 2761 florets on 21 capitula) under conditions of closed pollination. Why this pentaploid should have a much higher fertility than pentaploids produced by F1 triploids or hexaploids is not clear, but probably a very rigid selection in favour of fertility had taken place to produce its parent, - the F_2 triploid S823(13r)L1. Presumably this selection operated at the genic or cytoplasmic levels rather than in terms of chromosome number. The most notable feature of the sequence S823(13r) → S823(13r)L1 → S823(13r)L1:1 was the reduction in the glandulosity coupled with an increase in a monocarpic growth habit. Four progenies of S823(13r)L1:1 were grown, and they continued this progression, appearing macroscopically to be eglandular, and dying shortly after seed production, showing a monocarpic habit very similar to S. viscosus (see Plate 13).

The four progenies of S823(13r)L1:1 were the F_4 generation (counting the triploid S. X londinensis as the F1). These four fell into two pairs, distinguishable morphologically mainly in that one pair (S823(13r)L1:1:2 and S823(13r)L1:1:3) had narrower capitula than the other pair (see Plate 17). This capitulum size character may have been

Plate 16 Pollen mother cell meiosis in a progeny of a triploid F_2 Senecio X londinensis:



A B

S823(8r):1 2n = 48

A and B are both aceto-lacmoid stained preparations of pollen mother cells, X 1000.

A apparently shows a restitution nucleus following anaphase I, with 48 chromosomes. B shows a stage prior to this, with the chromosomes separating following metaphase I, a number of multivalents are apparent, by virtue of their size.

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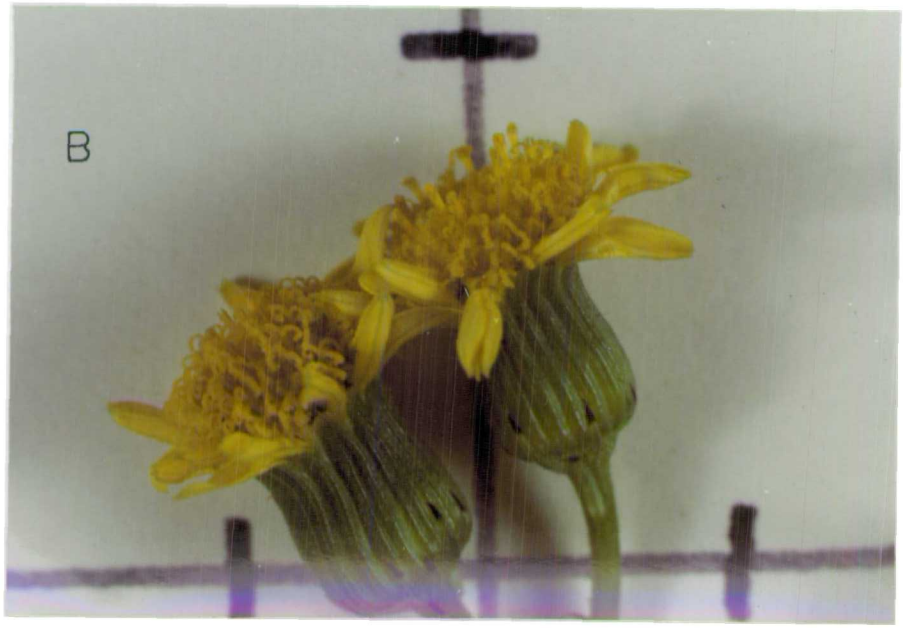
correlated with chromosome number, for the former two plants had chromosome numbers of 2n = 43, and the latter two of 2n = 44. Additionally, the two pairs of plants were characterised by different leaf shapes, one with pronounced auricular development and an elliptical outline, the other by tending more towards being spathulate (see Figure 23). Also, the

Plate 17 Capitula of advanced derivatives from Senecio squalidus X S. viscosus:

A = S823(13r)L1:1, 2n = 48, a derivative from S823(13r)L1 - an F2 triploid (2n = 30).

B = S823(13r)L1:1:1, and C = S823(13r)L1:1:2, both being derivatives from S823(13r)L1:1, in S823(13r)L1:1:1 2n = 44, in S823(13r)L1:1:2 2n = 43. Both are F4 hybrids if S. X londinensis is counted as an F1.

The Plates are X 3.3; the background scale being in cm..



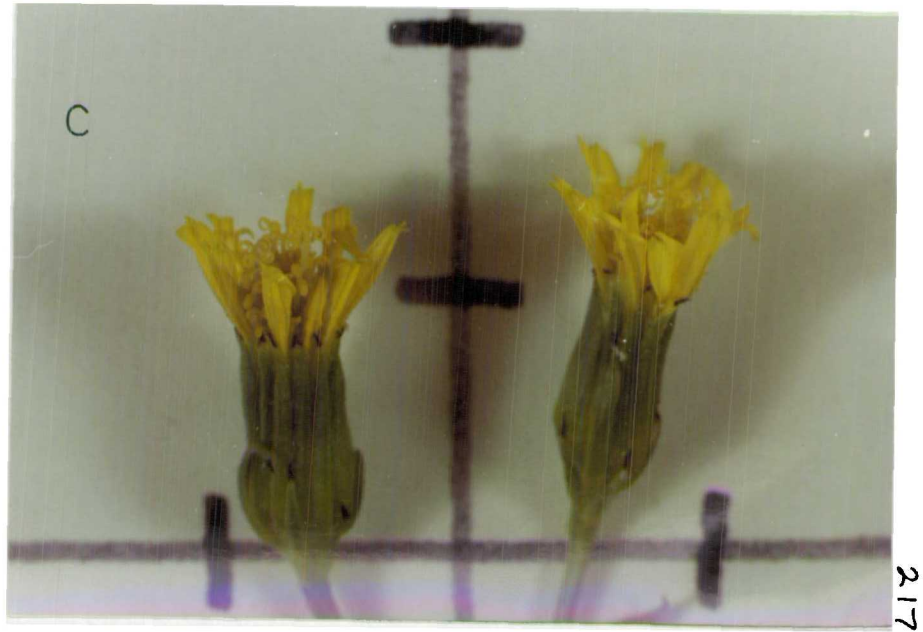
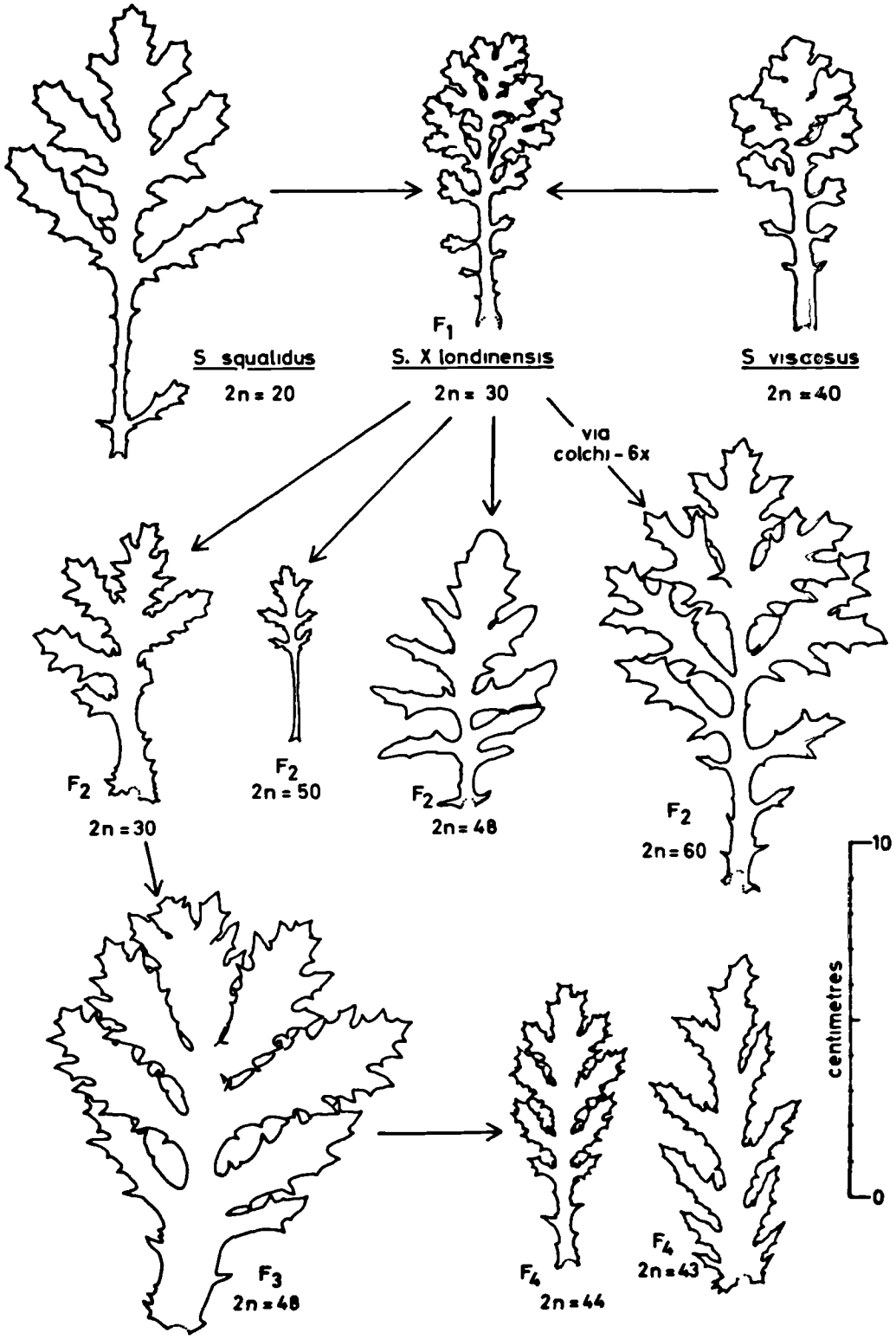


Figure 23 Leaf outlines in Senecio viscosus, S. squalidus, their F_1 hybrid, and the progenies of such a hybrid:



2n = 43 plants were mildew susceptible, while the 2n = 44 plants were not. The difference of a single chromosome was not responsible for noticeable differences in pollen stainability or size (see Table 39), or differences in seed set (see Table 44). These degrees of fertility of pollen and seed show a marked increase over the parent S823(13r)L1:1.

The sequence through four generations has therefore been characterised by a great increase in fertility and a tendency towards the tetraploid chromosome level. In addition, there has been a tendency towards certain parental characteristics: a lack of glandular hairs, and mildew susceptibility, as in S. squalidus; and the monocarpic habit, as in S. viscosus. In other features, such as those of the achenes and the ligules, there has been no obvious tendency towards either parental extreme. The achenes of the S823(13r)L1:1 progeny were light brown in colour, with short hairs in the grooves. The ligules of these plants retained the intermediate colour of the original F_1 hybrid, and were still of intermediate length, but they were tubular for some of their length, a character of neither parent. The close similarity in every respect of the progeny of S823(13r)L1:1 indicates that selection for viability has followed specific lines, and it would be interesting to see if other progenies of S. X londinensis, in tending towards fertility, followed the same morphological sequence.

Theoretically, the sequence of development of the S823(13r) family could have taken place under natural conditions, for at no point were these plants experimentally

Table 44 Seed set and length in the progeny of S823(13r)L1:1

plant code	no. capitula	no. seeds	no. seeds set	% seeds set	mean no. florets per capitulum	length of set seed in mm. mean	s.d.	range	no. seeds measured
S823(13r)L1:1:1	2	234	36	15.4	117.0	2.64	0.09	2.2 - 2.8	11
S823(13r)L1:1:2	27	1074	247	23.0	39.8	2.43	0.12	2.1 - 2.6	40
S823(13r)L1:1:3	19	936	48	5.3	49.3	2.78	0.13	2.3 - 3.1	16
S823(13r)L1:1:4	9	852	53	6.2	94.7	2.59	0.07	2.4 - 2.8	20
TOTAL	57	3096	374	12.1	54.3	2.56	0.17	2.1 - 3.1	87

treated. My finding at Barmouth of the F_2 triploid S823(8r) suggests that at least some products of the F_1 hybrids can develop. There have, however, been no records, and I have found no herbarium specimens of other plants which could have belonged to this sequence. The possible exception is one anomalous plant (in MANCH, from Derbyshire, 1865) which was more probably S. aegyptius, a Saharan endemic, but may have been a highly pollen-fertile segregant from some hybrid combination of Senecio species.

If this or a similar sequence of hybridity could give rise to plants which were cross fertile with S. viscosus, introgression could take place into that species from S. squalidus. Evidence for introgressed genes in S. viscosus is absent, although possibly some of the characters previously discussed as linking S. viscosus and S. sylvaticus could have originated in S. squalidus. With our present state of knowledge we cannot tell, but the higher fertility

Table 45

Reproductive biology of Senecio squalidus, S. viscosus, and S. vulgaris:

	S. squalidus	S. viscosus	S. vulgaris
flowering period (in calendar months)	(1-) 3-11 (-12)	(4-) 5-10 (-11)	(1-) 3-11 (-12)
pollen production	copious	sparse	very sparse, as low as 8 grains per locule; but var. hibernicus often has more
nectaries	present and functional (1)	present (2)	present and functional (1)
ligules	large and conspicuous	small and inconspicuous	usually absent; if present, small and inconspicuous
breeding system	self-incompatible and more or less exclusively outbreeding	self-compatible and inbreeding	self-compatible and more or less exclusively inbreeding
habitat	waste ground, arable land, roadsides, railway tracks and associated cindered areas, etc.; all three species often occur together		

(1) fide Percival, 1961; (2) fide Knuth, 1908

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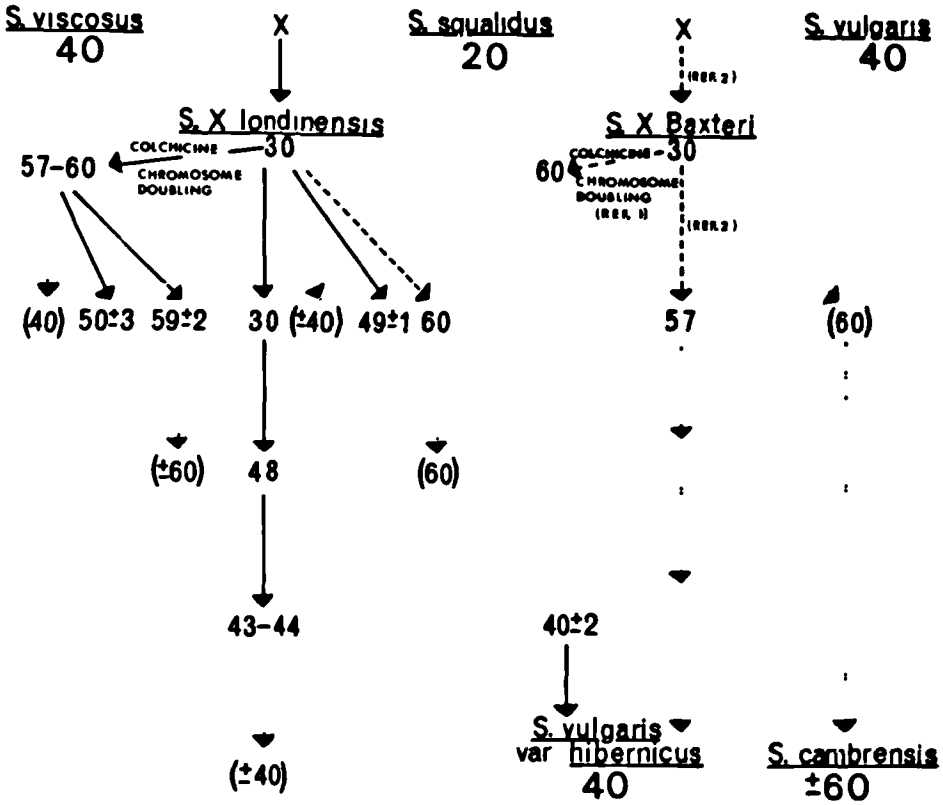
shown by S. viscosus/S. sylvaticus hybrids suggests that any introgression into S. viscosus has been from S. sylvaticus.

The importance of this work is less that it might suggest that introgression has taken place into S. viscosus, than that it shows the mechanism which could be involved. Thus, the triploid F_1 hybrid between the two Senecio species has given rise after a few generations to highly fertile plants of the more or less tetraploid chromosome number. Could the same have happened with S. squalidus and S. vulgaris? Could this

be the way in which S602 (the tetraploid hybrid of S. squalidus and S. vulgaris) originated? The similarity is worth noting between the sequence with the S823(13r) family of S. squalidus X S. viscosus and what apparently occured with progeny of the S. squalidus X S. vulgaris hybrid produced by Vosa in Oxford (see pp. 155-6 and Figure 24). Figure 24 gives a comparison of the postulated genetic relationships between S. squalidus and S. viscosus and S. vulgaris. Their relative reproductive biologies are given in Table 45.

Figure 24

Substantiated and hypothesised portions of the introgression sequences from Senecio squalidus into S. viscosus and S. vulgaris:



KEY. Numbers on the Figure are somatic (2n) chromosome numbers, if bracketed they have not been observed but may reasonably be expected to occur.

Solid lined arrows (——→) indicate that this step in the sequence has been relatively frequently observed; dash lined arrows (- - - - →) that it has been observed only on a solitary occasion, or very rarely; and dot lined arrows (· · · →) that it has never been observed, although it probably does occur.

REF. 1 is to the work of Harland (1953); and REF. 2 to that of Canio Vosa (personal communication).

SENECIO X VISCIDULUS

The hybrid between Senecio viscosus and S. sylvaticus was described by Scheele (1844) as S. X viscidulus. Lousley (1954) first described the hybrid from Britain, and quoted several reports of the hybrid from continental Europe. S. X viscidulus appears to be fairly common where the two species meet: Lousley (loc. cit.) suggested that the late recognition of the hybrid in Britain was due to the spread of S. viscosus from coastal and fen habitats, which has only occured recently.

Appendix Table 16 includes records of S. X viscidulus from herbaria seen by me. These specimens are characterised by being more or less intermediate between the parental species, and a comparison of S. viscosus, S. sylvaticus, and S. X viscidulus is given in Table 46. The hybrids are mostly seed sterile, but occasionally a low seed set is apparent, and I was fortunate enough to obtain live seed material from one of these specimens (ex Longiddry, in LIVU).

Plants grown from this seed were designated the S203 line. I performed little work on them, but the high seed set of the plants (see Table 47) would seem to indicate that S. sylvaticus and S. viscosus are occasionally genetically continuous.

Morphologically, the 20 plants of the S203 line grown remained recognisably intermediate between the parental species. The chromosome number of three of these plants was assessed as the same as the parental species : tetraploid, with 2n = 40.

Table 46 A comparison of the differences between Senecio viscosus, S. sylvaticus, and their hybrid S. X viscidulus:

character		S. viscosus	S. X viscidulus	S. sylvaticus
trichomes:	glands	very abundant	abundant	usually abundant
	clubs / whips	occasionally present	common	common
leaf:	colour	dark green	intermediate	yellow green
	shape (middle cauline)	deeply pinnatifid	intermediate	deeply and irregularly pinnatifid; often tapering towards apex
	lobes	equal; toothed or pinnatifid	intermediate	unequal; toothed
	auricles on upper stem	small or absent	intermediate	large
capitulum:	shape	conical	intermediate	cylindrical
	size	10 - 12 x 8 mm.	8 - 10 x 6 - 7 mm.	7 - 9 x 5 mm.
corymb		large and flat topped	intermediate	large and irregularly rounded
outer involucral bracts		ca. $\frac{1}{2}$ length of inner	variable, $\frac{1}{4}$ - $\frac{1}{2}$ length of inner	$<\frac{1}{4}$ length of inner
ligules:	number	(8 -) 13	8 - 13	8 - 13
	length	4.6 - 6.1 mm.	intermediate	ca. 2 - 4 mm.
achenes:	length	2.7 - 4.2 mm.	generally abortive, if set: ca. 2.5 - 3.5 mm.	ca. 2.5 mm.
	colour	yellow to black	if set: black	dark green
	hairs	usually glabrous, otherwise slightly hairy in grooves	short hairs on ribs	hairy on ribs

Table 47 Seed set under conditions of open pollination in material derived from Senecio viscosus X S. sylvaticus:
(The original plant (S203) resembled the F_1 hybrid; the Table gives seed production in two progenies of this plant)

plant code	no. heads	no. seeds per head			% seed set per head		
		mean	2 X SE	range	mean	2 X SE	range
S203:1	9	62.1	2.8	52 - 67	17.2	6.6	7.8 - 37.1
S203:2	8	68.0	2.3	59 - 74	16.9	7.0	3.0 - 32.3

An accidental S. squalidus ♂ X S203 ♀ hybrid was found to have the expected triploid chromosome number of 2n = 30.

Pollen mother cell meiosis in plants of the S203 line produced at metaphase 6 - 10 multivalents, with usually no, but occasionally up to three, univalents. This indicates that S. viscosus and S. sylvaticus differ from each other by a considerable degree of chromosome re-arrangement.

S. viscosus and S. sylvaticus are each uniform species with little intra-specific variation, although both, in common with S. vulgaris, show considerable modification in size and numbers of stems, leaves, and floral parts under different environmental conditions (Palmblad, 1968; Kumler, 1969). Herbarium specimens of each species show a marked constancy, which, in view of the regularity with which their hybrids have been found and collected, probably reflects a real lack of "off types" in nature. I have found a few variants, and these are listed in Table 48. These variants may owe their origin to several possible sources. The characters may be part of the ancestral variability of S. viscosus, with the localisation of genes resulting from inbreeding. Alternatively they may be

Table 48 Variants of Senecio viscosus:

locality	date	source	comments
Flookburgh, Westmorland	1967	My own collection and observations	An otherwise normal plant with short (ca. 2.5 mm.), yellow achenes. It bred true for these achene characteristics. A considerable variability in achene length (ca. 2.5 - 4.0 mm.) is exhibited by specimens of S. viscosus in the herbaria; but it is very rare for the colour of achenes to be lighter than black or dark brown.
Wrexham, Denbighshire	1968	CHR; and my own observations	A plant with ligules of a deeper yellow than normal, nearer to the colour typical of S. squalidus. Progeny grown by me from this herbarium specimen also expressed the deeper yellow ligules, but were otherwise normal S. viscosus.
Glasgow	1890	DBN	A specimen with markedly hairy achenes. This is a character often present in S. viscosus when the achenes are inspected closely, but very seldom to the extent of the Glasgow specimen.
Sent as seed from the Skopje, Yogoslavia Botanic Gardens	1968	My own observations	Plants showed the "club" and "whip" trichomes on the leaves and stems, as well as the glandular hairs, which are usually exclusive in S. viscosus.

the products of introgression from other species, such as via S203 type plants from S. sylvaticus, or from S. squalidus (which is discussed on pp. 219 - 221, in the context of fertile segregants from S. viscosus X S. squalidus). It is noteworthy that several of the characters in Table 48, such as hairy, small, and yellow achenes, and the occurence of "club" and "whip" trichomes are typical of S. sylvaticus.

DISCUSSION

The recent advent of *Senecio squalidus* into the British flora gives the opportunity to study several phenomena of flowering plant evolution in progress. Firstly, the British *S. squalidus* is of hybrid origin, and has become a widespread and common plant. A wide geographical separation from its parental species must effectively prevent genetic exchange between them, allowing evolution at the diploid level to be observed. Secondly, *S. squalidus* has been contributing genes to the native, tetraploid *S. vulgaris* with the result that a recognisably distinct taxon has evolved within the tetraploid species. Thirdly, *S. squalidus* and *S. vulgaris* have recently hybridised to form *S. cambrensis* which is stable at the hexaploid level, and which is segregating morphologically so that distinct taxa may evolve. These phenomena: neo-diploidy, introgression, and polyploidy are examples of the three basic mechanisms that Lewis and John (1963, p. 371) describe as leading to restoration of normal sexual reproduction following hybridisation.

All of these phenomena give the possibility of observing rapid evolution in progress, but raise taxonomic problems, as essentially unstable taxa are involved. My own interpretations of the taxonomy of these situations are given in the relevant Chapters in the text. By their nature, there cannot be simple, standard, taxonomic treatments of taxa recognised as having originated in hybridisation.

Each case must be accredited on its own merits, and any taxonomic treatment in a rapidly evolving taxon may be considered an interim measure, although still valuable. This discussion deals with evolutionary situations similar to those I have described in Senecio, and any taxonomic treatments they have been accorded.

1. HYBRIDISATION AND EVOLUTION AT THE DIPLOID LEVEL

The production of fertile progenies following hybridisation at one chromosome level can lead to several different evolutionary and taxonomic situations. These can be approximately divided into three categories: the introgression of genes from one taxon into another by back-crossing; the formation of hybrid swarms which may form a continuous series between the taxa involved; and the form--ation of taxa distinct from either parental taxon. Which evolutionary course is followed is due basically to the degree of isolation between the parental and hybrid taxa. Taxonomic assessment is often a reflection of the longevity and fecundity of the hybrids, - that is, how many generations have been involved - within the limits of the prevailing isolation.

Thus, hybridisation between tree species gives many situations where the long-lived nature of the plants results in considerable hybrid swarms occurring, often leading to an intergradation of the parental species. In Britain, many hedgerows contain hybrid swarms of Crataegus monogyna X

C. oxycanthoides; the London Plane is a hybrid swarm derived from Platanus occidentalis X P. orientalis (B.M.G. Jones, personal communications); and Quercus robur and Q. petraea intergrade (Cousens, 1965). In the cases of Crataegus and Quercus hybrid swarms are so extensive in some areas that "parental species" are rarely met with, and are possibly not representative of the parental species, but are segregants showing, by chance, the characters by which the species are distinguished. The situation in Platanus is different, for the parental species are geographically isolated from their hybrid swarm. In this case the London Plane has been given the name P. acerifolia, and more recently P. X hybrida (Jones, 1968). The importance of isolation is exhibited here not only in the evolutionary sense, but also because taxonomic distinction can be given.

Amoungst shorter-lived species clear examples occur of hybrid swarms existing for shorter lengths of time, even though they may often be formed. Their frequent but transitional occurence may make them easily recognisable on a morphological basis, and hence classifiable, despite often being sympatric with one or both parental species. The situation on Mt. Etna with Senecio aetnensis X S. chrysanthemifolius (= S. X incisus) is an example, and can be equated with cases in the same genus in Britain, - S. jacobaea X S. cineraria (= S. X albescens, see p. 276), and S. jacobaea X S. aquaticus (= S. X ostenfeldii, see p 276); and with examples such as Geum urbanum X

G. rivale (= G. X intermedium, reviewed by Briggs and Walters, 1969, pp. 183 - 193), where hybrid swarms are regularly formed when the species meet.

Senecio squalidus sensu lato illustrates the importance of geographical isolation in both evolution and taxonomy. In Sicily hybrid swarms between S. aetnensis and S. chrysanthemifolius can be given taxonomic recognition only as S. X incisus on the basis of morphological differences. These hybrid swarms form the early material for introgression between the two species by backcrossing and selection. Senecio is similar to Geum in this respect. Material in Britain, however, despite being morphologically analogous to S. X incisus, can be treated as a separate species, S. squalidus sensu strictu. This is because it is both geographically isolated from the parental species, and it has evolved over the course of many generations to a state where it is morphologically distinct from either of them, although still polymorphic and in general intermediate between them. Contrast this with Platanus: the London Plane is isolated from both parents, but still is treated only as a hybrid swarm (P. X hybrida). This reflects the longer evolutionary scale that S. squalidus has had available: I estimate that this amounts to at least three times as much in P. X hybrida (see footnote).

.....

footnote: This is based on generations of between about 2 per year and 1 every 3 years since 1700 for Senecio (giving between 100 and 500 generations), and between about 1 every 10 to 100 years since the 17th. Century for Platanus (that is, between 3 and 30 generations).

2. INTROGRESSION BETWEEN CHROMOSOME LEVELS

There have been few reports of introgression between taxa of different euploid (or nearly euploid) chromosome levels, and in several of these reports the mechanism involved is unclear. Nearly all recorded instances have been of gene flow from a lower to a higher chromosome level, as is the postulated case with *Senecio squalidus* and *S. vulgaris*.

Evidence of introgression of this nature has been obtained by the following workers: Raitanen (1967) found an intergrading between *Veronica longifolia* (2n = 34) and *V. spicata* (2n = 68) in Finland, including a tetraploid (2n = 68) plant resembling *V. longifolia*. Schöfer (1954) suggested that introgression was taking place in Europe from *Viola reichenbachiana* (2n = 20) into *V. riviniana* (2n = 40). In the same genus, Moore (1959) showed that introgression was occurring in North America between *V. riviniana* (2n = 40) and *V. lactea* (2n = 58). In the genus *Betula*, Elkington (1968) showed that the variability of *B. pubescens* (2n = 56) in Iceland tended towards *B. nana* (2n = 28) when compared with the British *B. pubescens*.

The majority of cases which have been experimentally investigated involve backcrossing between the F_1 hybrid (of intermediate chromosome number between the parents) and the parent of the higher chromosome number:

Boulos (1961) crossed *Sonchus uliginosus* (2n = 36) with *S. arvensis* (2n = 54), and from backcrosses obtained F_2

plants with 2n = 37 - 52. He noted that the two species were genetically continuous, and suggested that they should be treated as a single species.

In the genus Leontodon, Finch (1967) recorded hybrids and backcrosses as occuring naturally between L. hispidus (2n = 14) and L. taraxacoides (2n = 8).

Wcislo (1964) reported three cytotypes of Caltha palustris in Eastern Europe with 2n = 32, 48, and 56. He noted that occasionally plants with 2n = 58, and 60 were found, but only in mixed populations of 2n = 32, and 56 cytotypes. This may indicate that introgression has been taking place, the anomalous chromosome numbers being the segregant products of hybrids between the different cytotypes.

Ladizinsky and Zohary (1968) noted that sympatric diploid (2n = 14) and tetraploid (2n = 28) species of the section Eubarbarae of Avena showed considerable overlap morphologically. They synthesised the triploid F_1 hybrid, which when selfed set 1-4 % seed, and when grown with the tetraploid produced 4 - 16 % set seed. The F_2's were very diverse in form, showing a range of chromosome numbers from 2n = 14 to 29, most being 2n = 26 - 29 (2n = 4x = 28). Both the more or less diploid and the more or less tetraploid plants showed greater meiotic regularity than the F_1 triploid or those F_2 plants with 2n = 16 - 26. Vardi and Zohary (1967) showed a very similar situation in Triticum. Here, introgression was again suspected into a tetraploid from a diploid. Wild triploids were found, which were back-crossed

to the tetraploid, successive generations of back-crossing and selfing resulting in a restoration of fertility at the tetraploid level. Also in the Graminae, Zohary and Nur (1959) found that natural triploids in the diploid/tetraploid Dactylis glomerata complex produced offspring consisting mainly of vigorous fertile tetraploids, which they suggested constituted stages in the flow of genes from diploids into tetraploids.

Matfield et al (1970) obtained F_1 hybrids with 2n = 42 from Potentilla erecta (2n = 28) X P. anglica (2n = 56). These F_1 hybrids produced F_2 plants with 2n = 41 - 51, which Matfield and her co-workers suggested could back-cross with P. anglica to give results similar to those observed in the field, where introgression had apparently been taking place.

Dewey (1970) showed that progeny from the F_1 triploid from Agropyrum spicatum (2n = 14) X A. dasystachyum (2n = 28) gave an F_2 generation following open pollination with 2n = 26 - 29 (more or less tetraploid), 2n = 32 - 35 (more or less pentaploid), and 2n = 41 (nearly hexaploid). He suggested that a course of events similar to this resulted in both introgression into the tetraploid A. dasystachyum, and in the formation of the additional tetraploid species A. albicans by segregation.

In agronomic research, a number of attempts have been made to introduce desirable characters by back-crossing inter-ploid hybrids. The high infertility and high genetic "impurity" of the products of this process have, however,

limited its usefulness. It is used in crops where a high degree of genetic uniformity is not required (as in fodder crops) or in crops where seed fertility is not important. In banana (Musa spp.) it is used to introduce disease resistance from other species, either into the existing triploid clones, or by the formation of seed sterile tetraploids (Shepherd, 1968). Pritchard (1965) back-crossed Sorghum almum (2n = 40) with diploid Sorghum species (2n = 20) hybrids into the tetraploid, obtaining F_2's with 2n = 30 - 46, the higher number being more fertile. Similarly, Hawkes (1962) back-crossed Solanum stenostomum (2n = 24) into S. tuberosum (2n = 48) via their triploid hybrid.

There have also been records of introgression into a higher chromosome level following the polyploidisation of the inter-ploid hybrid. Most of this work appears to be agriculturally based. Gerstel (1945) succeeded in transfering virus resistance from Nicotiana glutinosa (2n = 24) into N. tabacum (2n = 48) via their experimentally produced allohexaploid (2n = 72) hybrid. Similarly, Parthasawathy and Kedharnath (1949) reported the transfer of "phyllody" disease resistance from Sesamum prostratum (2n = 32) into S. orientale (2n = 52); and Saunders (1965) introgressed Gossypium hirsutum (2n = 52) with genes of G. raimondii (2n = 26). In all of these cases, the artificially produced allopolyploid was repeatedly back-crossed into the higher ploid parent.

Outside of crop plants, Böcher (1962) suggested that the hexaploid derived from the triploid (2n = 54) hybrid of Epilobium angustifolium (2n = 36) and E. latifolium (2n = 72) may act as a bridge for gene flow between the species, although both species also occur in both diploid and tetraploid forms.

Another fairly well documented method is by the immediate production of F_1 hybrids at the same chromosome level as the parent of the higher ploidy. Thus, Pritchard (1965), and Hadley and Mahan (1956) quote diploid X tetraploid Sorghum species giving rise to both tetraploid and triploid F_1 hybrids, the tetraploids being more fertile than the triploids. Hermsen (1966) also noted tetraploid F_1 hybrids as well as triploids in Solanum bulbocastanum (2n= 24) crossed experimentally with S. acaule (2n = 48). These tetraploid hybrids were also of higher fertility than the triploids. Also in Solanum, Marks (1966) noted that diploid crossed with autotetraploid S. chacoense produced predominantly tetraploid hybrids. This, Marks suggested, was due to the break down in the gametophytic self-incompatibility system due to competition of the two S alleles in the diploid pollen. The result was a "triploid block": with the preferential production of tetraploid hybrids where a diploid donated both haploid and diploid pollen to tetraploid parents. In this case, the "triploid block" was effective at the pollen inhibition stage, in accordance with the "incompatibility sieve" hypothesis of

Lewis (1944), which coupled unreduced pollen with self-pollination in plants with gametophytic incompatibility systems. Similar results to those of Marks were noted by Woodell and Valentine (1961) in diploid and autotetraploid Primula, and by Lewis (1967) with diploid and autotetraploid Delphinium. The theory of the "triploid block" can be extended, although there is little experimental proof that it can occur outside of the specialised cases outlined above: it is possible, for example, that the balance of chromosome numbers in embryo, endosperm, and sporophyte may be important. In common with Primula, Senecio apparently has a sporophytic mode of incompatibility, and such a system does not respond with self-compatibility to the production of unreduced pollen. This is because the reaction of the pollen is determined by the sporophyte, and the gene complement of the pollen is of less importance. Thus, although Senecio would probably not respond as Marks' Solanum did, it may share with Primula a "triploid block" mechanism separate from the pollen/stigma reaction.

One example has been reported which may reflect a natural situation where tetraploid F_1 hybrids may be produced directly by a species cross: Olden and Nybom (1968) stated that both diploid and autotetraploid Prunus avium, when crossed onto tetraploid P. fruticosa could give rise to variable tetraploid F_1 hybrids, including some similar to the tetraploid species P. cerasus.

In the context of inter-ploid introgression, several

reports have been made of potential gene flow from higher ploids into lower ploids in experimental material. All of these reports have been of segregation or back-crossing from F_1 hybrids of inter-ploid chromosome numbers. They include Delphinium diploids and autotetraploids (Lewis, 1967); Sorghum diploid and tetraploid species (Hadley and Mahan, 1956); Triticum vulgare (2n = 42) X Agropyrum elongatum (2n = 70); Potentilla diploid and tetraploid species (Matfield et al, 1970); and Avena diploid and tetraploid species (Ladizinsky and Zohary, 1968). Natho (1959) reported Betula humilis (2n = 28) and B. pubescens (2n = 56) hybrid material occuring naturally in Europe at both chromosome levels, but the precise status of these hybrids is unclear.

The postulated mode of introgression from Senecio squalidus (2n = 20) into S. vulgaris (2n = 40) is via the triploid hybrid and back-crossing method already demonstrated in Dactylis, Avena, Triticum, Agropyrum, Sonchus, and Leontodon. The possibility also exists that the Senecio vulgaris X squalidus allohexaploid (S. cambrensis, 2n = 60) may back-cross into S. vulgaris, but there is no field evidence for this. There is no evidence to suggest that any kind of "triploid block" may be operative in the species of Senecio investigated.

There is no evidence that introgression may have occured from tetraploid species of Senecio into the diploid S. squalidus.

A point to be stressed from the Senecio work in the general context of hybridisation, and especially of inter-ploid introgression, is the importance in evolutionary terms of events which may occur very rarely. In Senecio, as in the cases quoted for Veronica, Viola, and Betula introgression occurs, but no or very few F_1 hybrids have been found; and if they have been synthesised at all, it was with difficulty.

The inter-ploid taxa in Senecio, apart from F_1 hybrids, being of such transitionary occurence have not been given taxonomic status: this reflects directly the situations in the inter-ploid hybrids in other genera described above.

3. THE ESTABLISHMENT OF AN ALLOPOLYPLOID SPECIES

Stebbins (1950, pp. 298 - 341) divided polyploids into categories according to the closeness of relationship of their parents. Gerstel (1956) reinforced this categoris--ation by stressing the importance of segregation in classifying new allopolyploids.

Senecio cambrensis behaves as the "true alloplyploid" of Stebbins (1950, pp. 326 - 332) would be expected to. It has a regular meiosis with slight multivalent formation, and (presumably) occasional allosyndesis results in segergation of parental, or novel, characters; and it is a clearly marked species. A more definite categoriseation cannot be made, for we know neither the ancestry of the population originally discovered by Green in 1948, nor the phylogenetic relationship between the parental species.

Since 1948, types have been found that have segregated slightly - to some extent transgressively - so that morphologically distinct races can now be said to occur.

The appearance of novel features in allopolyploids (indeed, in all types of hybrids) is a feature which confuses taxonomy and evolutionary pathways. In the category of "novel characters" must be included non-adaptive and deleterious characters. The few of these aberrant types which persist due to favourable selection are the "novel characters" of the new taxon. Aberrant types are a well known feature in progenies of hybrids: Gerstel (1956) quoted several examples in a range of new allopolyploids; and Goodman et al (1969) recorded aberrant segregants from the new natural allopolyploid Spartina alternifolia X maritima. To these examples can be added the loss of the black involucral bract tip character in S. cambrensis.

It is difficult to establish the cause of novel characters. Stebbins (1950, p. 329) suggested occasional allosyndetic pairing may result in them in allopolyploids. Lewis and John (1963, pp. 335 - 336) extended this hypothesis, when explaining aberrant types arising in the allopolyploid Primula kewensis, to consist of occasional multivalent formation, crossing over within them, and errors in their disjunction.

4. FUTURE POTENTIAL RESEARCH IN SENECIO

The establishment of the hybrid *Senecio squalidus* in Britain, and its relationships with *S. vulgaris*, give opportunities to apply established methods of taxonomy and the new techniques of population study to unique systems, and may yet reveal much about the importance of breeding systems, mutation frequency, and the effects of selection in the establishment of new taxa at different ploidy levels.

APPENDIX

CULTURE TECHNIQUES

Standard techniques were utilised in the growing of plants. Seeds were sown on the surface of John Innes No. 1 seed compost in a pot, pan, or box, and were covered with a sheet of glass to increase humidity and prevent stray seeds from being introduced. A sheet of newspaper was used to cover the glass in order to prevent direct sunlight heating the container. Germination rates varied, but generally germination was rapid and almost complete. No marked dormancy period was noted for the species involved. Hybrid, and other experimental seed, however, varied considerably in the time taken to germinate, and frequently a lapse of 3 months or more was noted between sowing and germination. In these cases late germination was usually associated with sickly plants, and thus was probably not a dormancy effect.

Seedlings were pricked out into J.I. No. 3 potting compost, and were grown to maturity in 3" to 4" clay or plastic pots. Plants required to flower rapidly (for example for fertility estimation, or genetic analysis) were grown in smaller pots (such as 2" plastic Multipots) in a sandy compost of 1 part sand to 1 part J.I. No. 3.

Subsiduary lighting to give about a 16 hour day was used if an increase in growth rate was required during the winter months in the glasshouse. None of the species involved exhibited any tendency towards a photoperiodic

control of flowering.

Monocarpic species did not benefit from repotting in order to increase axillary growth, and they could not be propagated by cuttings. Polycarpic species, and hybrids involving polycarpic material were amenable to both treatments. Cuttings were usually of stems involving 2 or 3 nodes. Rooting hormone (Seradix 2) was used, and cuttings were struck in J.I. No. 1 under polythene cover or mist on heated benches. Basal or axillary leafy shoots could be similarly treated.

The species were grown in glasshouses, and suffered from sundry pests and diseases. The occurrence and treatment of these are given in Appendix Table 1.

Appendix
Table 1

Control of insect and fungal pests of *Senecio* spp. in the glasshouse:

Pest	Comments	Treatment	Comments
Leaf miner (*Phytomyza atricornis*)	became at times a persistent and damaging pest	Lindane or Malathion sprays; or DDT/Lindane smokes at weekly intervals	only fully successful against adult flies, not against other stages
		physical destruction of larvae and pupae inside leaves by removal of leaves or *in vivo* squashing	time consuming and even more damaging to plants
various lepidopteran larvae (not identified)	never a serious problem	picked off by hand	
aphids (species not identified)	if not treated became a damaging pest	Malathion and Metasystox sprays as necessary	the control was effective
grey mould (*Botrytis cineraria*)	caused damp--ing off in seed boxes, and of pricked out seedlings	Captan and Thiram (Wettable) watered on as necessary	the control was effective
powdery mildew (species not identified, but probably *Erysiphe* spp.)	caused general lack of vigour in certain non--resistant taxa (e.g. *S. vulgaris*)	Karathane (Wettable) spray as necessary	repeated applications were often necessary, but were usually successful

HYBRIDISATION TECHNIQUE

The diploid species studied were self-incompatible: this including S. squalidus, S. chrysanthemifolius, S. aetnensis, and S. vernalis. The tetraploid species, S. vulgaris, S. viscosus, and S. sylvaticus were self-compatible, as were fertile hybrids between the diploid and tetraploid species (including S. cambrensis).

Hybridisation between the diploids was usually simply a matter of rubbing open capitula together in order to reciprocally transfer pollen. This did not produce 100% hybrids using the British S. squalidus as female, as this species showed a degree of selfing (see Appendix Table 2).

Hybridisation involving the tetraploids with the diploids presented greater difficulties. This was due to the self-compatibility of the tetraploids where they were treated as the female, their low pollen production when used as the male, and cross-fertilisation barriers between the species (see pp. 149-161).

Other workers have largely relied upon the self-incompatibility system when hybridising members of the Compositae, with any 'selfs' being recognised on morphological grounds. This is the method used in breeding such horticultural crops as chrysanthemums and dahlias, as well as in wild species, such as those of Haplopappus (Jackson, 1962) and Taraxacum (Richards, 1970).

Use has also been made of male sterility, which is often associated in the Compositae with florets of differing

Appendix Table 2 Hybridisations involving Senecio squalidus s.l., showing degrees of self-fertility in the British taxon as opposed to the Sicilian taxa:

parents		treatment	% seed set	total no. analysed	%	
♀	♂				maternal	hybrid
squalidus	vernalis	heads rubbed together	90	25	52.0	48.0
vernalis	squalidus		90	2	0	100.0
squalidus	viscosus		ca. 1	40	62.5	37.5
viscosus	squalidus		95	ca. 100	ca. 98	ca. 2
squalidus	vulgaris		ca. 1	12	100.0	0
vulgaris	squalidus		95	ca. 1000	100.0	0
squalidus	cambrensis		ca. 1	3	100.0	0
chrysanthemifolius	aetnensis		90	ca. 50	0	100.0
aetnensis	chrysanthemifolius		90	ca. 50	0	100.0
viscosus	squalidus	emasculated	ca. 1	13	38.5	61.5
vulgaris	squalidus		0	-	-	-
cambrensis	squalidus		ca. 1	9	77.8	22.2

ligulate character from the hermaphrodite florets. Thus, eligulate, male sterile African marigolds (Tagetes erecta) are used as female parents for the production of F_1 hybrids for horticulture (L.E. Watts, personal communication). Most of the Senecio species involved in this study have possessed peripheral, ligulate, pistillate florets in the capitulum; the disc florets being hermaphrodite and eligulate. Removal of the hermaphrodite florets, so that just the female, ligulate florets were left was attempted. A degree of success was met with, but the removal of 70 - 90% of the florets of the capitulum usually resulted in its death, and any apparently good seed formed by cross pollination onto the female florets rarely germinated. Male sterility was employed by Harland (1954) in order to produce the triploid F_1 hybrid S. X baxteri by pollinating a mutant S. vulgaris (the "dwarf strap" discussed on pp. 163-4) with S. squalidus.

Trow (1912) in hybridising S. vulgaris races relied upon heterotic vigour in the F_1 hybrid seedlings in order to screen for them, but this method is unreliable. Oliver (1911) suggested blowing pollen off open capitula by using a jet of water, followed by careful drying and then cross-pollination. He worked with lettuce (Lactuca sativa) and Helianthus, and with a few modifications the same method is used today in lettuce breeding. Lettuce, however, has considerably larger florets than Senecio, and only 12 - 15 florets per capitulum, compared with up to 100 in the self-compatible Senecio species. The difficulty with working

with florets this small, and the centripetal sequence of anthesis of the large number of florets renders this method impracticable in Senecio, due to the continuous liberation of pollen.

Emasculation in various forms has also been attempted. I attempted to kill pollen, or upset its development, by injecting water at temperatures rangeing from 50°C. - 100°C. with a hypodermic syringe into the cavity formed by the involucral bracts at an early stage of development of the capitulum. Plack (1952) tried dipping capitula at various stages of development into 30 - 37 % alcohol for 10 seconds. In both my own and Plack's experiments with S. vulgaris a very low success rate in inducing pollen sterility or in producing hybrids by subsequent cross pollination was obtained. In the case of the hot water treatment a high degree of pollen abnormality was only obtained at the expense of severe damage to the capitulum resulting in no seed being set.

Another emasculation method is that of removing the tubular petals of the florets complete with their adherent anthers by pulling gently. This method can be successfully applied to lettuce, but resulted in removal of the entire floret in Senecio.

The method outlined by Ornduff (1964) for Senecio lautus was the one which gave best results. Ornduff noted that in his species at a time in the capitulum ontogeny the anthers were borne above and clear of the style. Emasculation was effected by slicing off the top of the

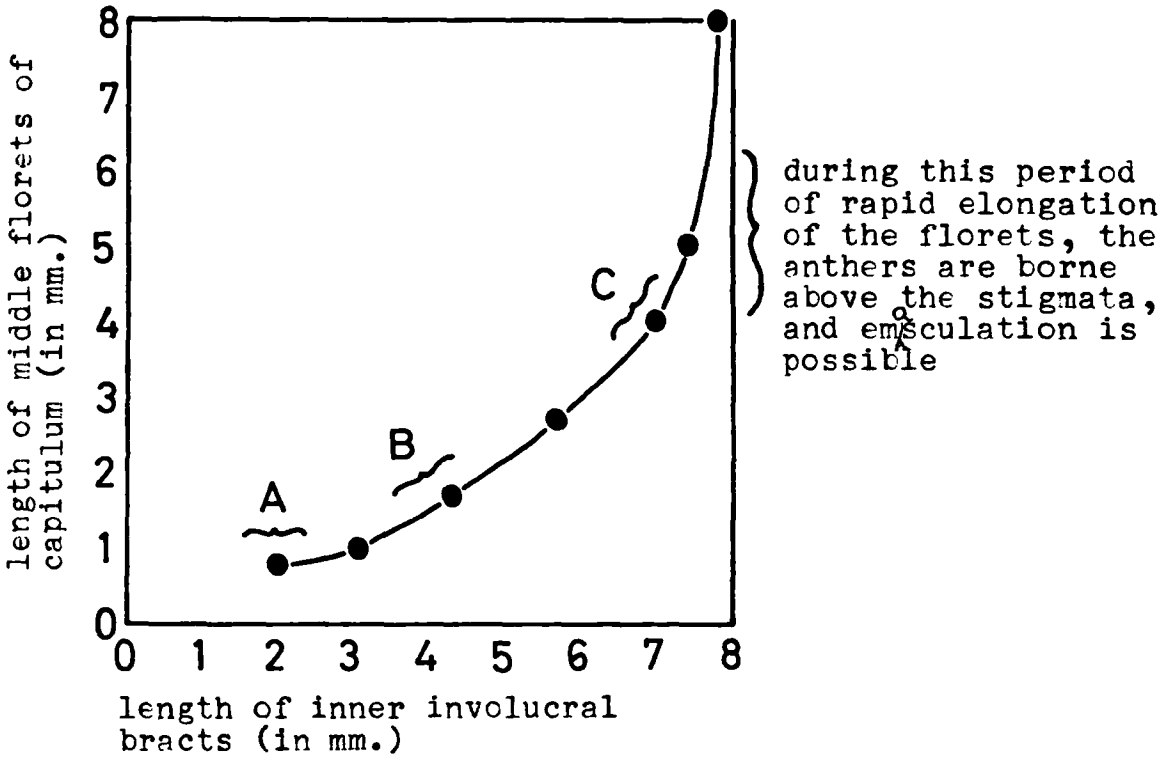
capitulum below the anthers and above the style. The styles emerged over the course of the next few days and were washed with water to remove stray pollen. Cross pollination was then effected repeatedly until the styles withered. This method was used on the tetraploid Senecio species of this study (see Appendix Figure 1), but could not be applied to the diploids, where the bottom of the anthers was at no stage above the tops of the styles. The problems with the method were the inherent damage to, and subsequent risk of death of, the capitulum. This particularly applied to S. vulgaris, which was very susceptible to disease. Also, it was difficult to emasculate at the correct level so that all anthers were removed while some styles were left intact at the centre of the capitulum, where they had developed least. The method was, however, quite successful using S. viscosus and S. cambrensis as the female parent, see Appendix Table 2.

Appendix

Figure 1

Floral ontogeny of Senecio vulgaris:

The graph shows the typical developmental pattern, points on the graph are from actual measurements. The length of the inner involucral bracts is, in effect, the length of the capitulum.



Stages in development:

A: Pollen mother cell meiosis

B: Pollen maturates; florets turn from white to yellow

C: Outer florets reach anthesis; anthers dehisce; style elongates

POLLEN TECHNIQUE

Pollen was dusted onto microscope slides for observat--ional purposes by dislodging pollen masses carried on the ends of newly emerged styles.

STAINABILITY

Aceto-carmine (see footnote) stained pollen rapidly, but due to its low viscosity and rapid evaporation of the acetic acid, there was a tendency for a segregation of stained and unstained grains within the slide. The unstained grains tended to accumulate at the edges of the cover slip, presumably because they were smaller and/or lighter than the stained grains.

Such a separation was not apparent when cotton blue in lacto-phenol (see footnote) was used. In addition, care was taken that a minimal amount of the liquid was used on each slide. Staining was sufficient after about 10 minutes of preparation of the slide for counts to be made from complete transverses of the slide. After the initial stages of this study, the cotton blue stain was used exclusively for stainability and size estimations.

Where possible, a minimum of 400 grains were counted in stainability estimates.

.....

footnote: Aceto-carmine 1 gm. carmine + 45 ml. glacial acetic acid + 55 ml. distilled water.

Cotton blue in lacto-phenol 1 gm. cotton blue + 25 ml. lactic acid + 25 ml. phenol + 25 ml. glycerol + 25 ml. distilled water.

Occasionally, in various pollen samples, groups of various grain size and frequency were seen of unstained pollen. These often occured in pollen otherwise of high stainability. These groups were ignored in assessments of pollen stainability in the belief that they were the result of some kind of accidental tissue death, and were not representative of the true pollen stainability.

SIZE

Pollen diameters were measured using a graticule eye--piece. Measurements were made across polar views of grains discounting the exine spines. Only stained grains were measured. Measurements were always made soon after mounting, and analysis of a representative group of these results is given in Appendix Figure 2, showing that there was no significant change in size (due to loss or gain of fluid content) during the course of these observations.

Where possible, 50 grains were measured in each sample. Occasionally, where the sample appeared to more than usually variable 100 grains would be measured.

In one series of measurements, discussed in the text, concerning the Sicilian taxa of S. squalidus, localised groups of larger grains were sometimes observed on slides. This was not, however, observed in material other than that from Sicily, and even in that case is probably due to somatic mosaicism rather than to artifacts in the mounting technique.

Appendix

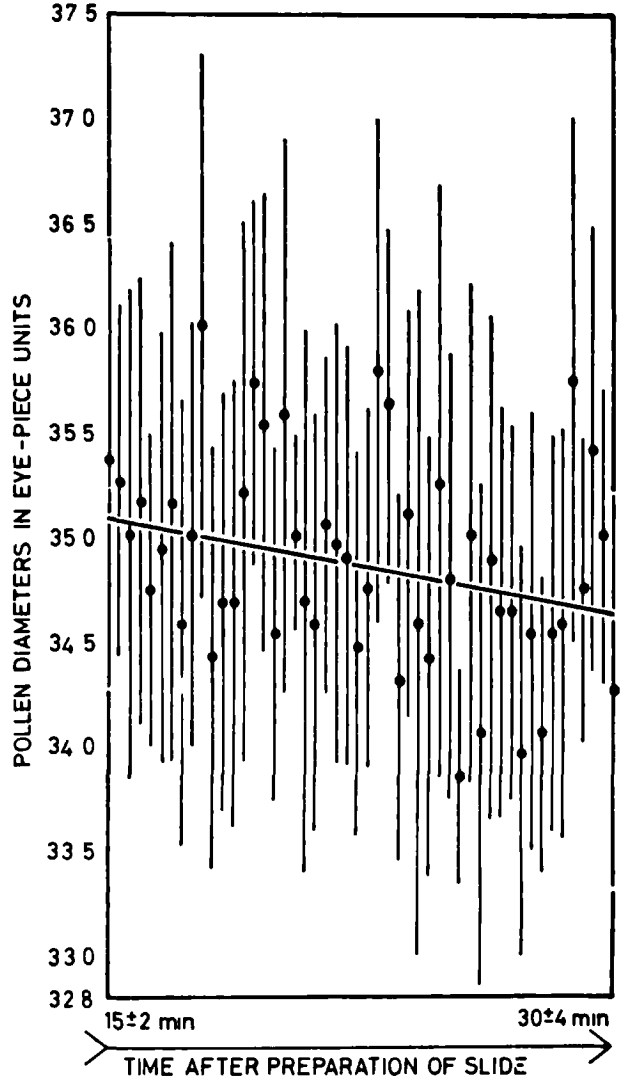
Figure 2 Stability of pollen diameters following cotton blue in lacto-phenol treatment:

(Results are from 19 members of the S602 family, and give means and 95% confidence limits of sequentially measured grains between 15 ± 2 and 30 ± 4 minutes after mounting, - a total of 950 grains being involved)

The estimated slope of the regression line is 0.0092, and the fitted line is y = 35.10 - 0.0092x, where y = pollen diameter, and x = time scale (in arbitrary units of 1 - 50); standard error of this line is 0.0047. This line represents a 0.45 eye-piece unit decrease in 15 minutes, which equals a 1.3% decrease, or less than 0.5μ.

Analysis of variance shows that this correlation between decrease in pollen diameter and time does not reach the 5% significance level:

	D.f.	S.s.	M.s.	V.r.
variation ascribable to x	1	0.88	0.88	3.82
residual variation	48	11.15	0.23	
total	49	12.03		



CHROMOSOME TECHNIQUE

Considerable difficulties were found in the study of chromosomes in the Senecio species. This is due in large part to the small size of the chromosomes, and in many cases to the fairly high numbers (where 2n = 40 or more). During the latter half of the investigation techniques had been evolved which at least allowed accurate counting of the chromosomes to be made. Studies of pollen mother cell (PMC) meiosis was only partially successful, and determinations of all of the meiotic configurations in a cell were seldom possible.

PMC PREPARATIONS

The selection of suitable capitula was a matter of experience for each species concerned. A rough guide was to use capitula at as large a stage as possible with the florets still green or white in colour before turning yellow (see Appendix Figure 1). Due to the centripetal sequence of development of florets in the capitulum, a few of the required stages could usually be found in each capitulum. There was no diurnal rhythm in the meiotic sequence, but it was found that adequate watering was necessary during the previous 24 hours in order to obtain cells undergoing meiosis.

MITOTIC PREPARATIONS

Attempts were made to study mitotic chromosomes in immature leaves and corollas, with limited success, and consequently virtually all work was performed on growing root tips. Again, no diurnal rhythm was noted in this tissue. Equally good results were obtained with clay or plastic pots,

the only problem being a tendency for root tips to adhere to the surface of the former type of pots unless watered just before extraction of the root ball.

PRETREATMENT

Aqueous solutions in various concentrations of acenaphthene, Aesculin, colchicine, chloral hydrate, paradichlorobenzene, ∝-bromonaphthalene and 8-hydroxyquin--oline were used to destroy the mitotic spindle, contract the chromosomes, and facilitate spreading. Treatments were attempted for various lengths of time from 1 - 24 hours and at various temperatures from 3 - 25°C.. With this large number of variables, and the difficulties with the material, these observations must to a large extent be traeted as circumspect. Within this context, only 8-hydroxyquinoline was found to give adequate results. The other chemicals failed because of the limited spreading, or appeared to reduce the staining of the chromsomes. Colchicine, in particular, caused good contracture of the chromosomes without reducing their stainability, but resulted in severe clumping of the chromosomes. The most successful method was the immersion of the root tips in a 0.02 M solution of 8-hydroxy--quinoline at room temperature (20 ± 5°C.) for 2 - 4 hours. Longer immersion, especially at the higher temperatures caused separation of the chromatids.

FIXATION

Carnoy fixative (6 ethyl alcohol: 3 chloroform: 1 glacial acetic acid), and acetic alcohol (3 ethyl alcohol: 1 glacial acetic acid) were found to be equally effective,

and in general the latter was used to fix both floral and root tip tissue. Floral parts were also often fixed directly in fatty acid based stains.

The formaldehyde based range of fixatives (for example: the Navashin fixative, see Sharma and Sharma, 1965) were found to be unsuitable because they restricted the subsequent softening of the cells necessary for good squashing, and often caused cytoplasmic staining.

HYDROLYSIS

Tissues were softened prior to squashing by the use of 1N hydrochloric acid. In the case of floral parts, a drop of HCl was added to the fatty acid based stain if this was used in a joint fixation/staining process, and gentle heat was applied, without boiling. Root tips were subject to hydrolysis in 1N HCl at 60°C. in a water bath as a prelude to Feulgen staining. It was found that the duration of this hydrolysis was not critical, although Feulgen cytophotometry might have revealed an optimum hydrolysis time (Mikshe, 1967). Usually a hydrolysis of 12 minutes was given on order to achieve maximum receptivity to the Feulgen stain without excessive degeneration of the tissue.

Pectinase (at 20 and 37°C., at aqueous concentrations of 1 and 5%) for durations of between 5 minutes and 5 hours was found to soften tissues to some extent, but offered little or no advantage either as an alternative or as a complementative to HCl hydrolysis.

STAINING

A number of chromosome stains were initially employed.

A slightly modified Feulgen technique, and the use of lacmoid (recorcinol blue) were finally selected as the best. Carmine and orcein (natural and synthetic), dissolved in 45% aqueous solutions of acetic, propionic, butyric, lacto-propionic and lacto-butyric acids (the latter two being 50:50 v.v. mixtures), with or without iron mordants, proved barely adequate both as direct stains of PMC's and as supplements following Feulgen staining. A few stains gave good chrom--osome staining, but also stained the cytoplasm excessively, these included crystal violet (1% and 0.5% aqueous solutions), fast violet (2% in 45% aqueous acetic acid), and haematoxylin (Wittman, 1965). Chlorazol black and chromosome red proved to be of no use in this instance.

The Feulgen technique initially was found to give little staining of chromosomes. This applied to Feulgen stain made up by the cold, or by the hot methods (Sharma and Sharma, 1965), and ready made Feulgen stain (Gurr's). I found that slightly better staining could be obtained by thorough washing to remove excess hydrolysis acid; and this advance was considerably improved upon by raising the pH of the Feulgen solution to above 2.5 by adding borax or NaOH (Lewis and John, 1964, p. 205; Dutt, 1968). The pH of the untreated Gurr's stain, and those produced by the Sharma and Sharma methods was between 1.6 and 1.8. The staining schedule finally in use is given in Appendix Table 3.

Observations were also made of nucleoli number, using

Appendix Table 3 Schedule for the staining of *Senecio* chromosomes: (A1 and A2 = alternative treatments for PMC meiosis in flower buds; B = treatment for root tips).

1. Potted plants watered well for preceding 24 hours	A1	A2	B
2. Material placed in 0.02M 8-hydroxyquinoline solution at 20±3°C. for 2 - 4 hours			B
3. Material rinsed in water, placed in fixative (3:1 or 6:3:1) at 20±3°C. for 30 min.	A1	(A2)	B
4. Material rinsed in water, placed in N HCl at 20±3°C. for 1 hour	A1		B
5. Material placed in N HCl at 60°C. for 12 min.	A1		B
6. Material rinsed for 3 min. in running tap water followed by rinse in distilled water for 5 min.	A1		B
7. Material placed in Feulgen stain (pH 2.5 - 4.0) at 20±3°C. in the dark for 1 - 3 hours	A1		B
8. Material rinsed in running tap water for 3 min.	A1		B
9. Material de-stained in SO_2 solution (50:50 v.v. N HCl and saturated aqueous $KHSO_3$): 3 changes of 5 min. each	A1		B
10. Material mounted in 45% acetic acid; or more usually in lacmoid fatty acid stain (1% stain in 45% aqueous acetic, propionic, lacto-propionic or lacto-butyric acids)	A1		B
11. Slide heated (not to boiling) in the lacmoid stain (as in 10.) plus a drop of N HCl		A2	
12. Material squashed on slide	A1	A2	B

the Feulgen/fast green method outlined by Sharma and Sharma (1965).

OBSERVATION

Cell squashes produced by the above method were observed using, at succeeding stages in the study, microscopes manufactured by Cooke, Troughton and Simms (the M 100); Meopta of Praha, Czechoslovakia; and Carl Zeiss (the Universal Standard). The only satisfactory photographs of chromosome material were obtained by using a Cooke, Troughton and Simms plate attachment to the Zeiss.

Slides required for further observation were made permanent by the usual method of floating off the cover slip and re-mounting in euparal after passing the slides through an alcohol series.

MICRODENSITOMETRY

Attempts were made to photometrically measure DNA quantities in nuclei of various species and hybrids used in this study. Observations were carried out on a Barr and Stroud Mark II integrating microdensitometer , using the Feulgen staining technique outlined by Mikshe (1967). Difficulties were encountered in the use of the machine due to a high degree of unrepeatability of the observations, although the technique appeared basically to be workable with this material. No worthwhile results were obtained.

I owe my gratitude to Professor C.D. Darlington, Dr. K.R. Lewis, and C.G. Vosa for both allowing me to use, and too for advising me in the use of this instrument at the Botany School, Oxford.

LIGULE DIMENSIONS

Ligule dimensions were always taken from capitula with as near to 13 ligules as possible. A minimum of 10 ligules were usually measured: length was determined with a transparent ruler on the upper surface of mature ligules to the nearest mm.; breadth was measured with a hardness testing lens (Brinall Magnifier) across the broadest part of the ligule to the nearest 0.1 mm..

CAPITULUM DIMENSIONS

Capitulum dimensions were taken from capitula with about two whorls of disc florets open. Means of 5 - 10 measurements were usually taken. The length of the capitulum was taken to be the length of the inner involucral bracts as measured to the nearest $\frac{1}{2}$ mm. with a ruler. The breadth of the capitulum was taken to be the breadth across the receptacular region, as measured to the nearest $\frac{1}{2}$ mm. with a ruler or a hardness testing lens.

MEASUREMENTS OF ACHENE LENGTHS

The lengths of fertile (set) achenes were measured, using a hardness testing lens which gave accuracy to 0.1mm.. Breadths were also measured, but gave variable results due to seeds occasionally being slightly flattened. While seed lengths are a useful measurement, I found that breadths only ranged from 0.4 - 0.6 mm., and have no apparent use as a taxonomic criterion.

Achene lengths showed some variability within the same plant. This was probably environmentally affected. An extreme example is given in Appendix Table 4, where seed was harvested on different dates from a series of plants grown from cuttings of a single plant (CS18). A t-test reveals highly significant (P = 0.1%) differences between all three different samples.

Thus, unless a comprehensive survey is made, or the conditions are carefully controlled, I doubt if achene lengths could be used for differentiating similar types, although the wide range of lengths shown by the Senecio aetnensis/chrysanthemifolius complex is apparently of use taxonomically. Achene length is clearly correlated with polyploid level in related plants. Appendix Table 5 gives compounded results which have been discussed in detail in the text: it should be noted that there is virtually no overlap of the ranges of the diploid and its autotetraploid, or of the triploid and its autohexaploid.

Appendix

Table 4 Length (in mm.) of fertile achenes of CS18 collected on different dates:

date collected	no. of seeds	mean	s.d.	range
21.6.68	20	3.99	0.13	3.6 - 4.2
1.7.68	13	3.49	0.14	3.3 - 3.7
24.9.68	20	3.73	0.19	3.4 - 4.1
TOTAL	53	3.77	0.25	3.3 - 4.2

Note: CS18 is a colchicine induced C_0 hexaploid from the triploid Senecio X londinensis.

Appendix

Table 5 Compounded results of achene length related to polyploidy in Senecio:

taxon	ploidy	no. of seeds	length, in mm.		
			mean	s.d.	range
S. squalidus	2x	65	2.47	0.13	2.1 - 2.7
	4x	151	3.34	0.30	2.7 - 4.2
S. X londinensis	3x	30	2.84	0.12	2.6 - 3.1
	6x	183	3.72	0.31	2.9 - 4.6

Note: The range for S. X londinensis is in fact greater than that shown in the Table: these figures refer to the only plant (S823(13r)) which was comprehensively studied, seed set being so rare, but the complete range shown for all 3x S. X londinensis achenes observed was 1.5 - 3.5 mm..

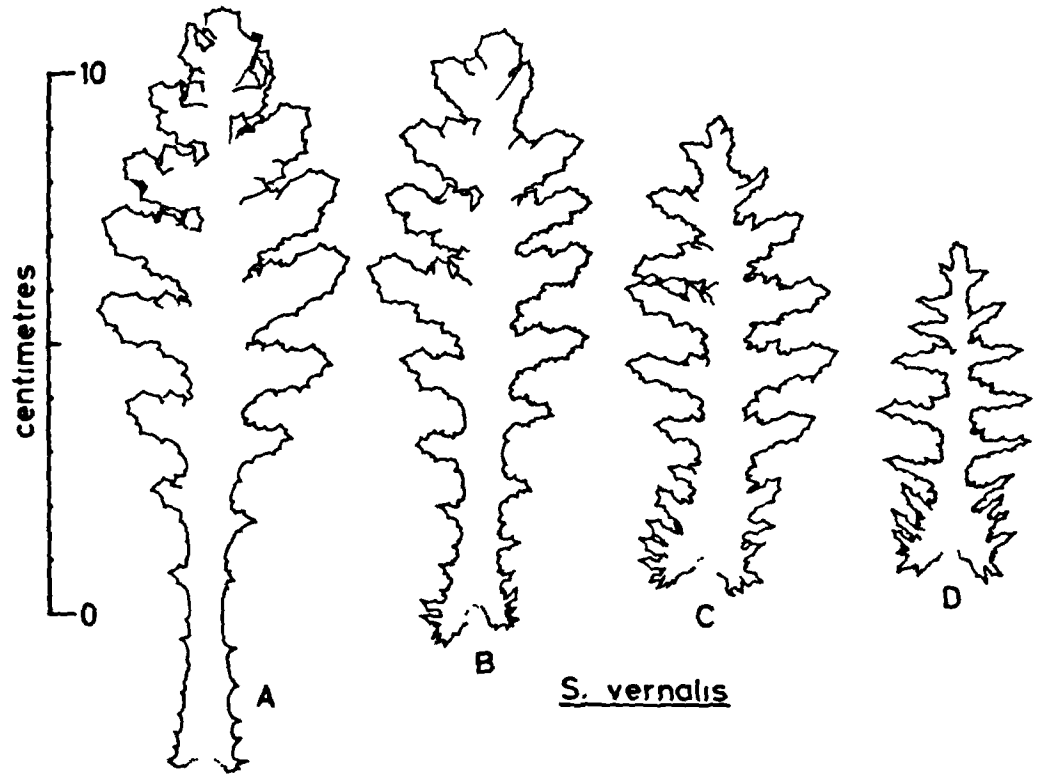
LEAF OUTLINES

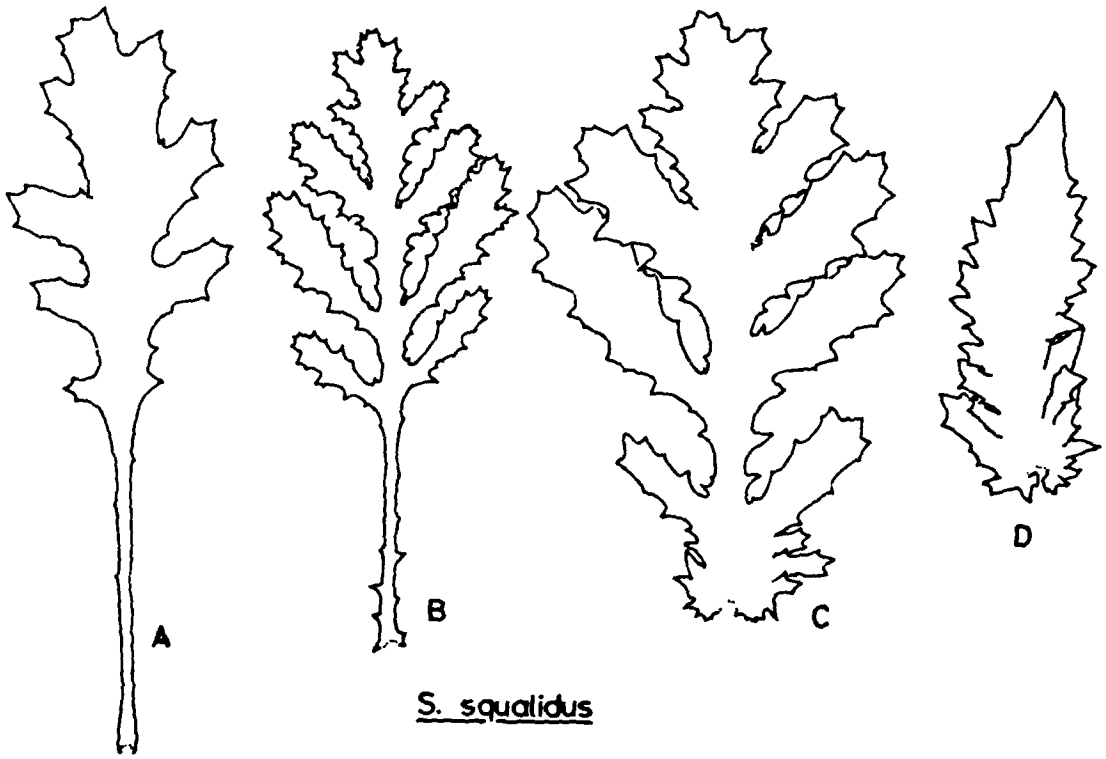
Leaf shapes were recorded by tracing the outlines onto transparent paper of pressed leaves. The use of pressed leaves removed confusion arising from contortions in the fresh material; and the use of outline drawings allowed an objective appraisal of leaf shape by removing masking characters such as colour and glandulosity.

The leaves used were carefully selected as being undamaged, and were always taken from the middle stem region: - below the flowering side shoots and above the basal or rosette leaves. Thus, in Appendix Figure 3 in both leaf series the leaf B would have been taken as representative. Leaf A of S. vernalis is a basal rosette leaf; leaf A of S. squalidus is similarly a basal leaf, but this species does not have a marked rosette. In both species, leaves C and D are taken from the flowering portion of the plant: C as a leaf on the main stem, from the axil of which was growing a flowering stalk; and D as a leaf on that stalk. C and D type leaves are very variable, and A type leaves are often missing. For these reasons middle cauline leaves (type B) were always used.

The leaves were pressed as carefully as possible tightly between plain cards inside an orthodox plant press in order to avoid contraction of the tissues. This method proved to be reliable.

Appendix Figure 3 Leaf shapes on single plants of Senecio species (explanation in text):





LEAF TRICHOMES

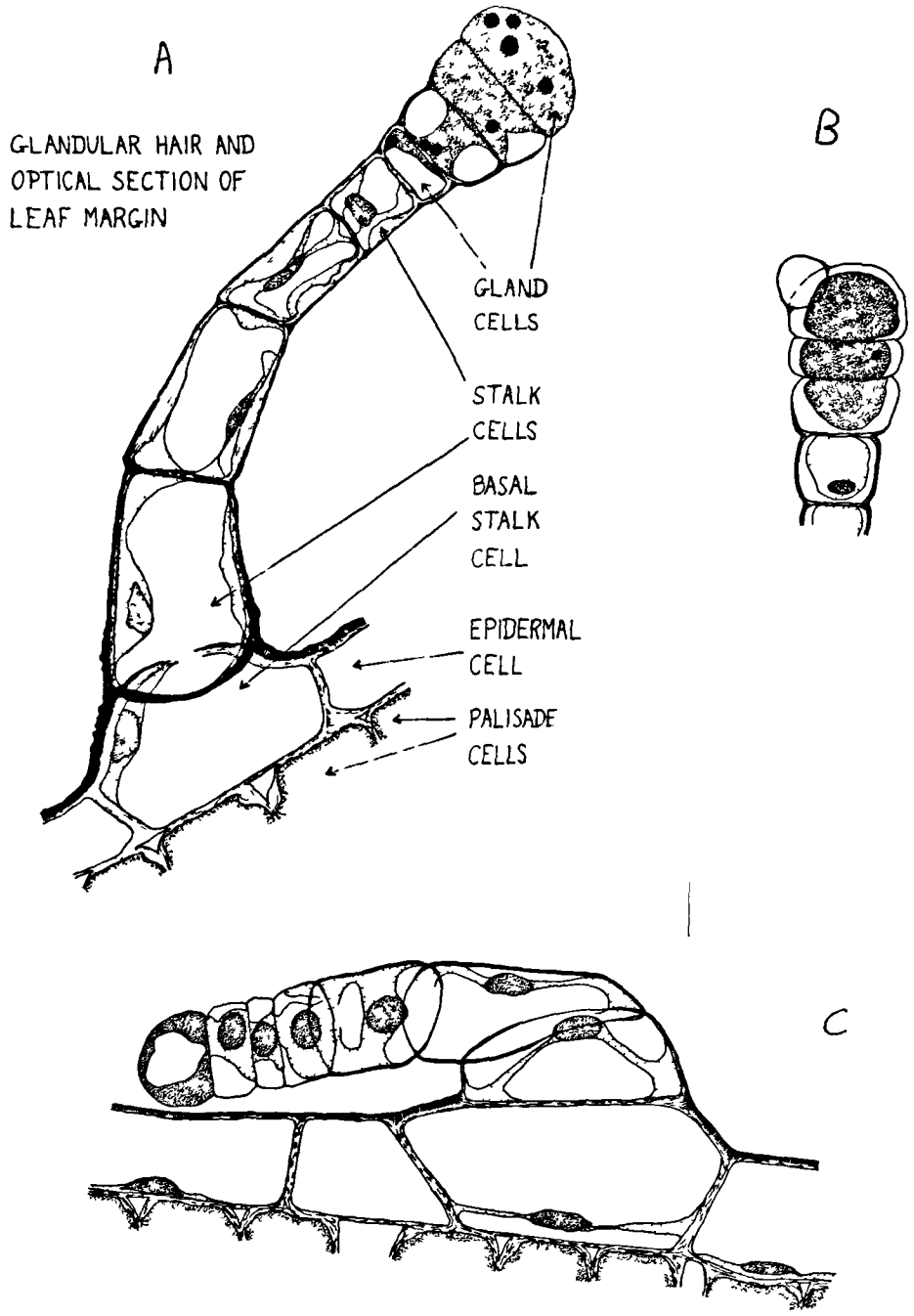
Drury and Watson (1965) investigated anatomical features in a broad spectrum of species in the genus Senecio. They noted the occurrence of several distinct and usually mutually exclusive morphological types of multi-cellular trichomes, corresponding to taxonomic sub-divisions in the genus. Usually the chief characteristic of these leaf hairs, achenial hairs, and pappus bristles was their terminal appendage. Drury and Watson worked principally from herbarium specimens, and their comments did not include the trichomes described below, which are best observed in fresh material. My method of observing these leaf trichomes was to mount a slice or scrape of epidermal material in cotton blue in lacto-phenol.

The leaf trichomes of the British Annui are of three types:

1. glandular (Appendix Plate 1)
2. non-glandular:
   a) with a bulbous terminal cell = "club" trichomes (Appendix Plate 2)
   b) with a long, slender and sinuous terminal cell = "whip" trichomes (Appendix Plate 2)

GLANDULAR TRICHOMES These consist of a basal cell in the epidermis, a stalk of 3 - 10 cells, and a head of 3 - 6 cells. Total length of glandular trichomes ranges from about 100μ up to about 500μ. They reach their largest in

Plate 1 Glandular trichomes from Senecio: (all are X 630)



A is from Senecio viscosus, and shows a trichome of the type found in this species, S. squalidus, S. aetnensis, S. chrysanthemifolius, S. sylvaticus, and S. vulgaris.
B shows a glandular head with a sub-cutaneous blister.
C shows a gland from a field grown S. vulgaris in which species the glands are often closely adpressed to the plant surface, and often lack the refractive globules in the glandular head.

the viscid species S. viscosus and S. sylvaticus. They are shortest towards the leaf teeth tips, and longest on the leaf lamina.

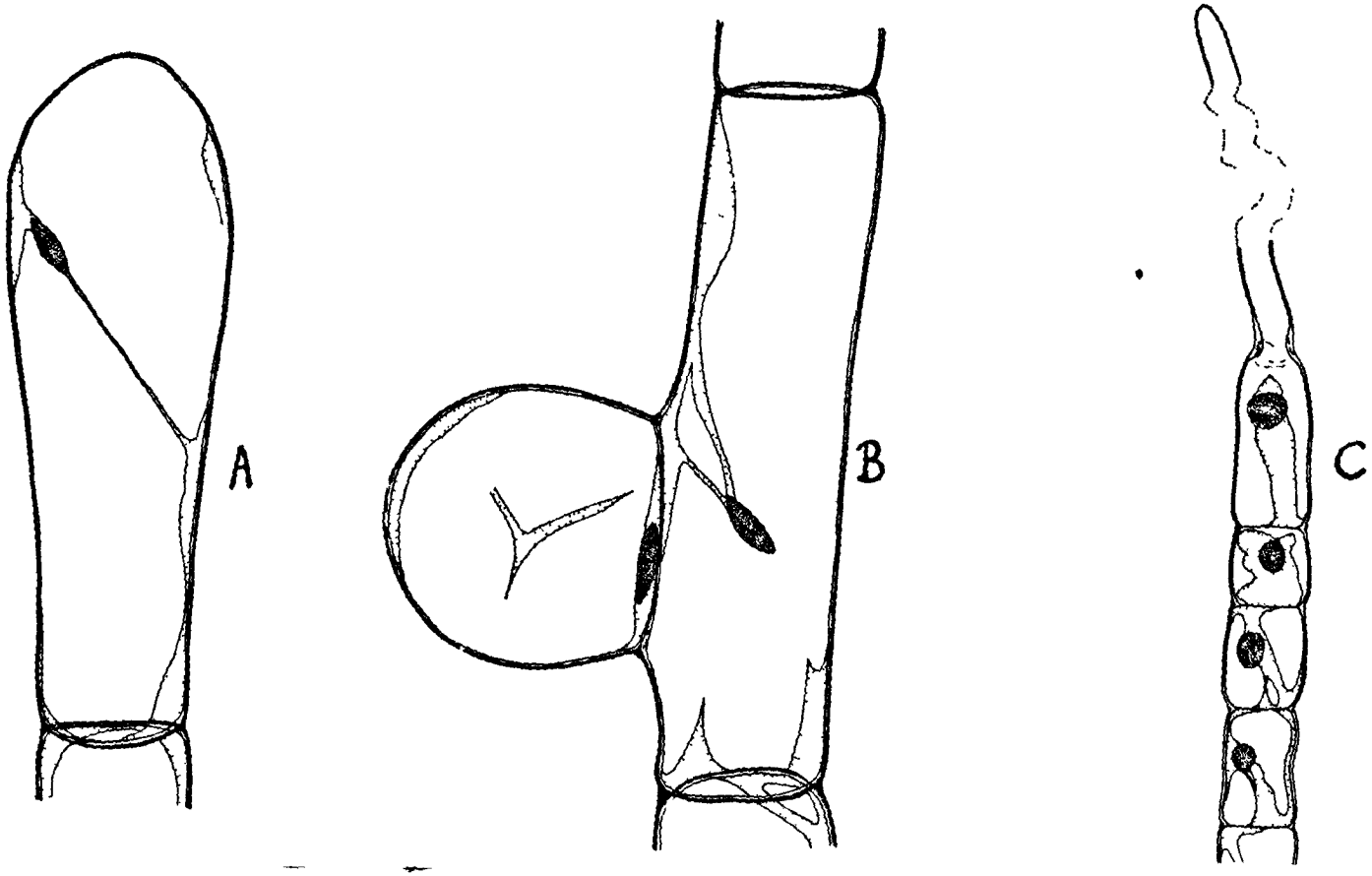
Stalk cells are often of the endodermal type that Stocking (1956) suggested to have a role in movement and accumulation of materials in gland cells. Certainly, endodermal type cells were most noticeable in those hairs which possessed refractive globules in their gland cells. The gland cells also have densely stained cytoplasms, obscuring the nucleus, if one is present. The character-istic smell of the viscid Senecios is probably due to volatile substances released from the glands by physical rupture. This smell, of a similar nature to that of Matricaria matricarioides ("stinking mayweed"), is variously described as "foetid", "aromatic", or "musky". The function of these secretions may be the prevention of insect attack, and they may well have fungicidal properties, for viscid plants are unaffected by the usual Senecio pests: leaf minor, aphids, and mildew. Merz (1959) reported an unidentified chemical in the glands of Senecio viscosus which inhibited the larvae of Euchelia jacobaea (the cinnabar moth) - a common pest of non-glandular Senecio species.

Glandular trichomes are usually distributed on stems, involucral bracts, petioles, and both surfaces of the leaves. They are often very plentiful on leaf margins. They appear to be fully developed at an early stage in leaf development.

NON-GLANDULAR TRICHOMES Club trichomes are up to 1 mm. in length, and consist of 3 - 20 large, thin-walled cells. Whip trichomes are considerably shorter, even with their long processes, which contributes about a half to their total length, and seldom exceed 400μ. They are composed of 10 - 20 cells, which are smaller than those of the club trichomes, and become progressively smaller towards the apex of the trichome. The basal cells of both types of trichome appear to be otherwise typical epidermal cells. Both types of trichome are distibuted on most aerial parts of the plants, with the exception of the floral parts although they occas--ionally occur sparsely on the involucral bracts.

The function, if any, of these two types of trichomes is not apparent. Club trichomes are formed early in leaf development, when whip trichomes are seen as chains of non-elongated cells with dense cytoplasm. Later, in more mature leaves, both these trichomes appear to be less frequent, probably due to their dispersion as the leaf expands, and to loss of trichomes by mechanical means. Many trichomes on mature leaves are dead and have broken ends.

Plate 2 Non-glandular trichomes in Senecio: (all are X630)



A is the terminal cell of a "club" trichome, the longest type of trichome found in these species. Drawn from Senecio squalidus, as are the other non-glandular hairs.
B shows a rarely found short side arm in a "club" trichome. True branching was not seen.
C shows the terminal cells of a "whip" trichome.

HERBARIA CONSULTED

Herbaria which I consulted are listed below together with their standard abbreviations derived from:

D.H. Kent, "Index to British Herbaria" Bot. Soc. Brit, Isles London, 1957

J. Lanjouw and F.A. Staflen "The herbaria of the World" Regnum Vegetabile 31 I.B.P.T. Utrecht, 1964

BIRA	Birmingham City Museum and Art Gallery
BIRM	Botany Department, University of Birmingham
BM	British Museum (Natural History), London
BRISTM	City Museum, Bristol
CAT	Botany Department, University of Catania, Sicily
CGE	Botany School, Cambridge
CHR	Grosvenor Museum, Chester
CRK	Botany Department, University College, Cork, Eire
DBN	Irish National Herbarium, Dublin, Eire
K	Kew
LIV	City of Liverpool Museum
LIVU	Hartley Laboratories, University of Liverpool
MANCH	Manchester Museum
OXF	Fielding-Druce Herbarium, Botany School, Oxford
SPT	Southport Botanic Gardens Museum
TCD	School of Botany, University of Dublin, Eire
UCNW	Department of Botany, University College of North Wales, Bangor

Appendix

Table 6 Native and established species of *Senecio* in Britain:

Species	Section	2n =	Habitat	Comments
S. squalidus L.	Annui O. Hoffm.	20	waste ground, etc., typically old walls and railway embankments	of Sicilian origin, now widely established in England, Wales and Ireland
S. vulgaris L.	"	40	waste ground, disturbed habitats, etc.	native, very abundant
S. viscosus L.	"	40	waste ground, sea shores, etc.	probably native; common and often locally abundant
S. sylvaticus L.	"	40	waste ground, especially sandy heaths and borders of woods	native, locally common
S. cambrensis Rosser	"	60	waste ground, old walls, etc.	native, the naturally arisen allopolyploid from *S. vulgaris* X *S. squalidus*, still restricted to the North Wales area
S. jacobaea L.	Jacobaea O. Hoffm.	40 (32)	pastures, waste ground, etc.	native, common and widespread
S. aquaticus Hill	"	40	wet meadows, stream sides, etc.	native, locally common and widespread
S. erucifolius L.	"	40	grassland and waste places, especially over calcareous or heavy soils	native, locally common and widespread
S. cineraria DC.	Incani DC.	40	mainly in coastal localities in England, Wales and Ireland	a South European maritime species, grown horticultur-ally in Britain and now established in several localities

- continued -

S. paludosus L.	Crociseris Reich.	40	fens	now extinct, although European material has now been introduced to the remaining fens
S. doria L.	"	40	wet meadows, stream sides, etc.	introduced, a Central European species now established in several localities in Britain
S. fluviatilis Wallr.	"	40	fens, stream sides, etc.	a species with a Eurasian distribution, now widely established in Britain
S. palustris (L.) Hook.	Tephroseris (Schur.) O. Hoffm.	48	fens	as S. paludosus
S. integrifolius (L.) Clairv.	"	48 (50)	1. calcareous grassland	locally common in South England
			2. maritime cliffs	local, Anglesea and Westmorland
S. mikanioides Otto ex Walp.	Scandentes	40 20	scattered localities	a South African species grown horticulturally in Britain
S. smithii DC.		80	coastal localities in Scotland	a South American species grown horticulturally in Britain
S. tanguticus Maxim.		80	scattered localities	a Chinese species grown horticulturally in Britain

Appendix
Table 7

Species of Senecio occasionally introduced into Britain:

species	n =	geographical origin	comments
S. vernalis W. & K.	10	Eurasia	a grain adventive; a member of the Annui
S. erraticus Bert.	20	Europe	frequently reported, but very close to S. jacobaea and S. aquaticus
S. barbariaefolius Krock.	20	Europe	
S. fuchsii Gmel.	20	Eurasia	
S. lautus Forst.	20	Australasia	both wool adventives; often confused
S. inaequidens DC.	20	S. Africa	
S. glossanthus (Sond.) Belcher		S. Africa	a wool adventive
S. pterophorus DC.	10	S. Africa	a wool adventive

Appendix
Table 8

Species of Senecio that have been recorded once or very rarely in Britain:

species	n =	geographical origin	comments
S. sagittatus Sch. Bip.		Asia	
S. cacaliaster Lam.	20	Asia	horticultural plant
S. clivorum Maxim.	30	Asia	horticultural plant; also placed in Ligularia
S. minimus Poir.	30	Australasia	a wool adventive
S. macrodontus DC.		Australia	a wool adventive
S. bipinnatisectis Belch.		S. Africa	a wool adventive
S. pinnulatus Thunb.		S. Africa	a wool adventive; taxonomically near to S. inaequidens
S. cannabinaefolius H. & A.		S. Africa	a wool adventive; taxonomically near to S. pterophorus
S. juniperinus L.		S. Africa	a wool adventive
S. lyratus L.		S. Africa	a wool adventive
S. arenarius Thunb.	9	S. Africa	a wool adventive; a member of the Annui
S. elegans L.	10	S. Africa	a horticultural plant; a member of the Annui
S. hieracioides DC.		S. Africa	a wool adventive
S. brasiliensis Lees		S. America	a wool adventive

Appendix Table 9 Hybrids reported in Britain involving Senecio species exclusive of the Annui:

Reported hybrid:	Source:	Comments:
S. jacobaea L. X S. cineraria DC. = S. X albescens Burbidge & Colgan	Reported on numerous occasions since 1836 (in CGE, from Bishops Castle, Salop.). Found in coastal regions of England, Wales and Ireland, and a few inland localities	Afrequent hybrid where the introduced S. cineraria becomes established. Hybrids are fertile, and back-crossing to both parents apparently takes place
S. aquaticus Hill X S. cineraria DC.	A specimen in the European section of MANCH labelled as occuring in Britain, no further details	Could just as well be a S. X albescens segregate
S. jacobaea L. X S. erucifolius L. = S. X liechten-steinensis Murr. = S. X whitwell-ianus Cheetham	Rep. Bot. Soc. & Exch. Club for 1909:415, a specimen from Yorkshire, comm. by C.G. Druce.	Said to have "facies of intermediate".
	Specimen in BM from Northants., coll. by Augustin Ley in 1910.	Morphologically intermediate
	Rep. Bot. Soc. & Exch. Club for 1906:229, two plants from Odiham, N. Hants., one with pubescent achenes, the other with glabrous; coll. by J.E. Palmer.	Druce suggested that these specimens were of S. nemor-ensis Jordan (Lor. et Barr. Fl. Moss. p. 337), - a variety of S. jacobaea.
	Rep. Bot. Soc. & Exch. Club for 1884/6: 129, two plants from Airton, M.W. Yorks., coll. by W. Whitwell.	One specimen said to be intermediate, the other nearer S. erucifolius.
	Rep. Bot. Soc. & Exch. Club for 1884/6: 129, from near Woodkirk, S.W. Yorks., coll. by F.A. Lees.	A speciem of S. erucifolius said to have a few characters of S. jacobaea.
S. jacobaea L. X S. aquaticus Hill = S. X ostenfeldii Druce	Reported on numerous occasions and apparently fairly common where the species meet. Specimens are in most herbaria. Recorded notably in Rep. Bot. Soc. & Exch. Club for 1943/4:823; Stewart and Corry, 1938; Praeger, 1951; and Kent, 1964(d).	Hybrids are variously reported as being sterile (the first reference), and fertile (the other three). The status of these species and S. erraticus requires clarification.

Appendix Table 10 Chromosome numbers of British Senecio spp. exclusive of the Section Annui:

Species:	n	2n	Reference:	Source of material:
S. jacobaea L.	20		Afzelius (1924)	Europe
		40	Böcher and Larsen (1955)	Eire, Denmark, Sweden, Norway, Poland, Germany, France
		32		Eire - dune race
		40	Mulligan (1959)	Canada (introduction)
	20		Ornduff et al (1963)	California (introduction)
	20	40	Crisp (unpublished)	counts from 3 British and 2 French populations
S. aquaticus Hill	20		Afzelius (1949)	Europe - as S. aquaticus Huds.
		40	Reese (1952)	Europe
		40	Crisp (unpublished)	Wales, one population
S. erucifolius L.	20		Afzelius (1924)	Europe
	20		Palmblad (1965)	Sweden
		40	Crisp (unpublished)	counts from 2 British populations
S. cineraria DC.	20		Afzelius (1924)	Europe
	20		Palmblad (1965)	French Mediterranean
		40	Crisp (unpublished)	counts of two plants from horticultural sources
S. paludosus L.	20		Afzelius (1924)	Europe
S. doria L.	20		Afzelius (1924)	Europe
		40	Quezel (1957)	Europe
S. fluviatilis Wallr.	20		Afzelius (1924)	Europe

- continued -

S. palustris (L.) Hook.	24	Afzelius (1924)	Europe
	48	Zhukova (1964)	Russia
	48	Zhukova (1966)	north east Russia
	48	Mosquin and Hayley (1966)	Arctic Canada
	24 25	Ornduff et al (1967)	Alberta
	48	Hedberg (1967)	Arctic Canada
	48	Johnston and Packer (1968)	Alaska
S. integrifolius (L.) Clairv.	24	Okabe (1931)	Asia
	46	Sokolovskaya and Strelkova (1938)	Russia
	48 90	Sokolovskaya and Strelkova (1941)	Russia
	48	Rutland (1941)	Britain
	24 25	Afzelius (1949)	Europe
	24	Rutland (1947)	Europe
	90	Sokolovskaya and Strelkova (1960)	Eurasian Arctic
	48	Zhukova (1966)	Russia
	48	Johnston and Packer (1968)	Alaska
S. smithii DC.	80	Afzelius (1924)	Europe (cultivated)
	80	Baksay (1958)	Europe (introduction)
S. mikanioides Otto ex Walp.	10	Ornduff et al (1963)	California (introduction)
	40	Harland, in Löve and Löve (1961)	Britain (introduction)
	20	Marchant (1968)	Britain (cultivated)
S. tanguticus Maxim.	40	Afzelius (1924)	Sweden (cultivated)

Appendix Table 11 First Vice County records of Senecio squalidus until 1930:

V.C.	year	locality	source and comments
23	1792	Oxford	CGE
37	1801	Worcester	Kent, 1956
(22)	?1803	Tilehurst	BM - associated with the railway, the date is obscure, and may be 1883. Tilehurst is close to the Oxford - Reading railway
(H4)	?1819	Cork	K - a Bot. Exch. Club specimen with an obscure date
H 3	1820	Bandon	Rep. Watson. Bot. Exch. Club (1900/1):20
5	1820	Taunton	Kent, 1956 - a deliberate introduction
4	1827	Bideford	Kent, 1956; BM; Devon Assoc. (1943) 75: 53 - 55, and (1944) 76: 43
(27)	?1827	Yarmouth	BM - the date is obscure
38	pre 1829	Allesley	Kent, 1956 - a deliberate introduction
83	1833	Edinburgh	Kent, 1955 - an escape from the Botanic Gardens, recorded again in 1890, and then not again in Scotland until the 1950's near Edinburgh (Kent, 1955 and 1966)
22	1833	Wytham	Kent, 1956
H 4	1839	Cork	Kent, 1956
34	1843	Bristol	Kent, 1956; K
25	1843	Gorleston	Kent, 1956 - a deliberate introduction
26	1849	Bury St. Edmonds	Kent, 1956
15	ca. 1850	Canterbury	Kent, 1956; 'G', 1873; - a deliberate introduction
27	1850	Eaton	Kent, 1956 - a deliberate introduction
53	1855	Anwick	Kent, 1956
21	1867	Twickenham	Kent, 1956 - introduced in ballast
32	1870	Bridgstock	BIRM
17	1867	Teddington	BM
11	1876	Bloxham	BIRM
7	1888	Pewsey	Kent, 1960 - associated with the railway
39	1889	Biddulph	Kent, 1960; LIVU; MANCH
60	1889	Durham	LIVU - a deliberate introduction

- continued -

H21	1889	Dublin	Irish. Nat. (1900):245
24	1896	Bletchley	Kent, 1960 - associated with the railway
41	1898	Cardiff	Kent, 1960
1	1899	Penzance	CGE
H 7	1899	Inchicore	Irish Nat. (1900):245 - spreading along the railway
29	pre 1900	Cambridge	Proc. Bot. Soc. Brit. Is.(1955) 1:471 - a deliberate introduction
9	1900	Portland	Kent, 1960
35	1904	Severn Tunnel	Kent, 1960; BM
6	1904	Portishead	BM; Proc. Bristol Nat. Soc. (1960) 30:111; Proc. Bot. Soc. Brit. Is. (1900) 3:377
40	1906	Linley	Kent, 1960; LIV; MANCH; Rep. Bot. Exch. Club (1906):229
43	1906	-	Rep. Bot. Exch. Club (1906):229
58	1910	Northwich	BIRM; CGE; MANCH; LIV; Rep. Bot. Exch. Club (1910):568-70
50	1910	Brymbo	Kent, 1960; OXF; K; - transfered with iron ore from Oxford, or by train from Warwick
	1910	Bidwilly	NMW
58	1912	Delamere	Kent, 1960; LIV
44	1912	Carmarthen	Kent, 1960; Rep. Bot. Exch. Club (1912):212
18	1913	Grays	Kent, 1960
2	1914	Par Harbour	Kent, 1960
5	1915	Taunton	BIRM - a deliberate introduction
16	1916	Grove Park	Kent, 1960; OXF; Rep. Bot. Exch. Club (1916):491
46	1916	Cardigan	Kent, 1960; OXF; Rep. Bot. Exch. Club (1916):491
3	1917	Exmouth	Kent, 1960
51	1917	Saltney	Kent, 1960
33	1922	Cheltenham	Kent, 1960
61	1923	Hull	K
42	1925	Talgarth	Kent, 1960
H14	1925	Maryborough	Kent, 1964 - associated with the railway
45	1927	Parrog	Kent, 1960
3	1927	Ratbey	Kent, 1960
20	1929	Hitchin	Rep. Bot. Exch. Club (1929):120
48	1930	Barmouth	Kent, 1960 - associated with the railway

Appendix Table 12 First Vice County records of *Senecio vulgaris* var. *hibernicus* until 1930:

V.C.	year	locality	source and comments
23	1832	Oxford	LIV
H 4	1849	Cork	BM
17	1879	Croydon	BIRM
58	1879	Oxton	LIV
4	1880	Bideford	BIRM
H 1	1882	Killarney	K
35	1883	Strenfreth Bridge	BIRM
41	1888	Kirkaldy	MANCH - this was cultivated material of unknown origin
H21	1894	Dublin	DBN
H35	1898	Baltimore	Phillips, 1898 - Phillips quotes these as *hibernicus*,
H34	1898	Skibbereen	but they may, from their locations, be maritime races
6	1900	Portishead	Rep. Bot. Exch. Club (1932):341
48	1900	Barmouth	NMW
38	ca.1900	Leamington Spa	BM
29	1901	Cambridge	Rep. Watson. Bot. Exch. Club (1901/2):15 - cultivated material of Cork origin. Also CGE; MANCH; LIV; and BIRM
H 3	1906	Bantry Bay	OXF
34	1906	Avonmouth	Rep. Bot. Exch. Club (1932):341
59	1910	?	OXF
H39	1912	Larne	Stewart and Corry, 1938; CGE; OXF
55	1915	Humberstone	Rep. Bot. Exch. Club 4 (1916):352
22	1915	Botley	OXF
46	ca.1916	Aberystwyth	Stephenson, 1946
15?	1920	Kingsdown	OXF - "Kingsdown" could equally well be in a number of alternative V.C.'s, such as 7, or 16
H 9	1924	County Clare	DBN
50	1926	Gwersyllt	Rep. Bot. Exch. Club (1926):118 } - unconfirmed reports of
39	1927	Burton-on-Trent	Rep. Bot. Exch. Club (1927):401 } *X Baxteri*, which are more probably *hibernicus*
33	-1929	Cheltenham	K
3	1930	Plymouth	K

Appendix Table 13 Probable records of *Senecio squalidus* X *S. vulgaris* (= *S.* X *baxteri*):

In view of the confusion between *S.* X *baxteri* and the ligulate varieties of *S. vulgaris* the Appendix only includes specimens either inspected by me, or identified by persons experienced with these taxa. Annual Reports of the Botanical Exchange Club have been abbreviated to RBEC; and the Botanical Society of the British Isles Year Books to BSBI Y.B.

V.C.	year	locality	comments	source
23	1884	Oxford	sterile seeds	CGE
23	1891	Oxford	det. G. C. Druce, sterile seeds	BIRM
22	1907	Reading	sterile seeds	BM
23	1911	Oxford		CGE
34	1927	Avonmouth	det. N. Sandwith	RBEC(1932):341
9	1930	Weymouth	sterile seeds	K
3	1941	Goodrington	sterile seeds	K
17	1943	London	sterile seeds	BM
27	1943	Norwich	det. E. A. Ellis	CGE; K; Howard and E.A.E. (1943)
27	1944	Norwich	6 plants	Ellis (personal communication)
21	1944	London	det. Sandwith	K
21	1944	London	solitary plant	RBEC(1945):60
34	1944	Bristol	det. Sandwith	RBEC(1945):60
9	1945	Parkstone	det. J. E. Lousley	BM
14	1946	Eastbourne	sterile seeds, det. Lousley	K; RBEC(1946):299
23	1946	Oxford	det. J. P. M. Brenan	K; BM; Brenan (1946)
63	1947	Sheffield	sterile seed	BM
18	1947	Walthampstow	det. Lousley and D. H. Kent	Lond. Nat. Suppl. (1953): 32
21	1948	Hounslow	det. Kent	K; Lond. Nat. Suppl. (1953): 32
21	1948	London	det. Sandwith	Lond. Nat. Suppl. (1953): 32
37	1949	Yardley Wood		BM
11	1949	Southhampton		BM
17	1949	Whitley	det. Lousley	BM
33	1949	Tewkesbury		BSBI Y. B. (1949): 61
63	1951	Sheffield	det. Lousley	BM; K; CGE; BSBI Y.B. (1952): 106
66	1958	Hurworth	det. J. W. Heslop-Harrison	Vasculum 43:7 (1958)
66	1959	Raishy	det. Heslop-Harrison	Vasculum 44:15 (1959)
21	1960	London	det. D. E. Allen	Lond. Nat. 41:21 (1961)
16	1962	Sevenoaks		CGE
26	?	Hildenhall		BM
41	?	Cardiff		BM

Appendix Table14 Details of specimens intermediate between Senecio vulgaris and S. squalidus until 1930, as recorded in Figure12a.

Reports are based on comments relating to recorded specimens, or on personally inspected herbarium material. Annual Reports of the Botanical Exchange Club have been abbreviated to RBEC. S602 refers to the naturally occuring fertile family of S. vulgaris X S. squalidus discussed at length in the text.

1. In the vicinity of Oxford:

V.C.	year	locality	comments	source
23	1867	Oxford	- as the short-liguled variety of S. squalidus, var. parviflorus Dyer. "Occurs sparingly amoung thousands of normal plants" - W. Thistleton Dyer.	K RBEC (1867):9
23	1886	Oxford	resembles S602, but near to S. vulgaris var. hibernicus; pollen regular	BM MANCH
23	1887	Oxford	"a rare form found around Oxford resembling S. crassifolius" - G. C. Druce	RBEC (1887):184
23	1891	Oxford	"S. crassifolius" - J. G. Baker; "S. X Baxteri" - Druce	RBEC (1891):337
23	1892	Oxford	"nearer vulgaris than others of these hybrids" - Druce	RBEC (1892):371
22	1903	Reading	discussed at length by Druce and W. O. Focke, who both noted hybrid characters and fertile seeds	RBEC (1903):
22	1915	Botley	"near S. crassifolius" - Druce; "large praecox type" - A. H. Trow (praecox refers to one of Trow's ligulate varieties of S. vulgaris)	RBEC (1915):352
22	1929	Didcot	"S. advena" - Druce (- a name used loosely by Druce to refer to plants of an intermediate nature); resembles S602	BM

- continued -

2. In the vicinity of Cork:

V.C.	year	locality	comments	source
H4	1819	Cork	an old specimen on which the date is not clear; resembles an S602/*hibernicus* intermediate	K
H4	1833	Kilbarrack	eligulate, hirsute, *squalidus* type leaves, *vulgaris* type heads; could be an S602 type	LIV
H4	1853	Cork	heads fairly large, otherwise intermediate, seeds set	CGE
H6	1861	Passage West	generally resembles *vulgaris*, but with *squalidus* type leaves, heads large, ligules broad and short, seeds small and set	DBN
H4	1867	Cork	nearer *hibernicus* than S602, pollen regular and fairly small	MANCH
H4	1873	Cork	"ripe seeds .... like ordinary *S. vulgaris* .... rays much longer and broader (than the Channel Island ssp. *denticulatus*)" - J. L. Boswell	RBEC (1873):27 RBEC (1879):15 Irish Nat. (1898):22
H4	1878	Cork	a very large plant: "*S. vernalis*" - Boswell; "var. *radiatus*" - E. Rosser. Cult. at Balmute? (could this be Balmuto, Edinburgh?). Probably an S602/*hibernicus* intermediate	BM OXF BIRM
H4	1879	Cork	an S602/*hibernicus* type; pollen large, mostly 3-pored, some unstained	MANCH
H4	1888	Cork	large heads, broad ligules, seed fairly large; otherwise resembles *S. vulgaris*	DBN
H20	1894	Greystones	a large plant with large heads, large achenes, and intermediate sized ligules. The leaves near *squalidus* type. Probably an S60? type of plant	DBN

- continued -

V.C.	year	locality	comments	source
H4	1896	Cork	a small, hirsute, erect S602 type with large heads	DBN
H	1899	Inchicore	"both species and their intermediate" - R. A. Phillips	Irish Nat. (1900):245
H4	1901	Cork	several plants: "hybrids approaching parents" - F. W. Burbidge. These are probably very close to var. hibernicus, although the ligules are fairly broad. The plants vary in head size.	DBN
H6	1901	Passage West	plant generally resembling vulgaris, but with squalidus type leaves; heads large; ligules broad and short; seeds small and set well.	DBN
H4	1902	Cork	several plants of the same type as the 1901 Cork (DBN) specimens	DBN BM
H4	1904	Cork	"S. hibernicus Syme" - Phillips. Resembles a small S602 type, hirsute, with large heads	DBN
H4	1904	Cork	9 small plants closely resembling depauperate squalidus, but with large, set seeds (up to 3 mm. long), and heads in tight clusters. Indistinguishable, as a herbarium specimen, from S. cambrensis.	DBN
H6	1907	Passage	large plant with large broad ligules, large heads, leaves resembling vulgaris type, seed set and of medium length	DBN
H4	1897	Cork	the date is not clearly stated for this specimen, quoted by Burbidge as being of the "hybrid range".	Irish Nat. (1897):300
3. In the Cardiff/Bristol area:				
41	1900	Cardiff	recorded as X Baxteri, which it resembles, but seed is set	K

- continued -

V.C.	year	locality	comments	source
41	1902	Cardiff	possibly S. squalidus, but heads clustered and small as in S. vulgaris	LIVU RBEC (1902):
41	1905	Cardiff	= specimen "B" of RBEC(1906): "achenes abortive" - Rosser; pollen large, some 4-pored, low stainability; ligules short and broad; leaves resemble squalidus type. Definitely an S602 type of plant	MANCH LIVU CGE RBEC (1906):228
41	1906	Cardiff	= specimen "C" of RBEC(1906): a large (0.7 m. tall) plant; ligules long and broad; leaves intermediate; seeds large; capitula in dense clusters. Another S602 type	BM BIRM CGE LIVU RBEC (1906):228
41	1906	Cardiff	= specimen "A" of RBEC(1906): heads large, with small ligules; leaves resemble those of S. squalidus; heads clustered, and the general growth form resembles that of S. vulgaris	CGE LIVU RBEC (1906):228
41	1906	Cardiff	"var. radiatus" (= var. hibernicus) - H. J. Riddelsdell. Several plants, one of which has heads and seeds too large for hibernicus. Probably a more advanced stage than the other Cardiff specimens noted here.	CGE LIVU RBEC (1906):228
41	1908	Cardiff	"S. nebrodensis" - Riddelsdell. Two typical S602 type specimens, one with leaves nearer to the vulgaris type	BM
6	1909	Portishead	resembles a very large specimen of var. hibernicus, seeds large	BIRM
6	1910	Portishead	" a form of squalidus" - A. H. Trow and G. C. Druce; "of hybrid origin" - E. S. Marshall and Riddelsdell. The CGE specimen appears to differ from S. squalidus mainly in its ligules being smaller than normal. Its correct identification remains in doubt	CGE RBEC (1910):568 - 570

- continued -

V.C.	year	locality	comments	source
6	1917	Portishead	resembles var. hibernicus, but with large seeds	BM
41	1927	Barry	"S. vulgaris X S. vernalis" - C. G. Druce, teste A. Thellung	RBEC (1927):401
41	1928	Cardiff	a specimen with eligulate "pom-pom" heads of the type that I observed in natural hybrid material at Birmingham, 1969	K

4. In the North Wales/Cheshire area:

58	1868	Bowdon	eligulate plant resembling S. vulgaris, but seeds and heads large	CGE
58	1910	Northwich	a plant with very small ligules resembling S. vulgaris, but with fairly large heads	CGE
50	1927	Wrexham	a plant with large heads; broad, short ligules; leaves near to the squalidus type; pollen large, 4-pored, and highly stainable. Could be an S602 type, or S. cambrensis. Note that the locality is within the present S. cambrensis range	MANCH
51	1928	Hawarden	resembles S. X Baxteri, but may be a later generation	BM
39	1930	Burton-on -Trent	"S. advena" - Druce. An S602 type	OXF

5. Others:

70	1890	Shelwith Bridge	a plant with heads resembling the squalidus type; heads in dense clusters; ligules short and broad; seeds large and well set; pollen large and regular	BRISTM
48	1894	Barmouth	2 plants: 1 ligulate, the other eligulate; leaves resembling the S. cambrensis type, noted as being "thick and fleshy"; heads large, otherwise resembling the hibernicus type; genral growth form of the S. squalidus type, but stunted.	K

Appendix Table 15 Records of *Senecio squalidus* X *S. viscosus* (= *S.* X *londinensis*) until 1965:

V.C.	year	locality	source and comments
16 17 18 21	1943 ↕ 1963	London	BM (24 specimens); K (22 specimens); records are also in the London Nat. Suppl. 32 (1953); Rep. Bot. Exch. Club (1945):162; Rep. Bot. Exch. Club (1946):299; Lond. Nat. 39: 56 (1956); Lond. Nat. 41: 21 (1961); and Lousley, 1944.
33	1922	Toddington	BM, recorded as *S. vulgaris* X *viscosus*
38	1945	Birmingham	K; BM; Rep. Bot. Exch. Club (1945): 162
3	1946	Goodrington	BM; Rep. Bot. Exch. Club (1946): 299
63	1947	Beighton	BM
63	1948	Beighton	Naturalist (1948): 26
39	1948	Norton Canes	BM; Trans. N. Staffs. F. C. 86: 82 (1952); Proc. Bot. Soc. Brit. Is. 1: 53 (1952)
25	1948	Felixstowe	BM; K
63	1951	Sheffield	BM; MANCH
63	1952	Sheffield	CGE
39	1953	Burton-upon-Trent	K
24	1954	Burnham Beeches	CGE; Proc. Bot. Soc. Brit. Is. 1: 498 (1954)
48	1960	Barmouth	K; Benoit (1960) also records it here in 1955 and 1956
16	1963	Sevenoaks	Proc. Bot. Soc. Brit. Is. 6:61 (1965)
22	1963	Abingdon	OXF; Proc. Bot. Soc. Brit. Is. 6:61 (1965)
37	1964	Flodbury	BM
83	1965	Borthwick Bank	BM
23	1965	Claydon Hay	OXF
83	1965	Edinburgh	Proc. Bot. Soc. Brit. Is. 6: 243 (1966)

Appendix Table 16 British records of Senecio viscosus X S. sylvaticus (= S. X viscidulus):

V.C.	year	locality	source and comments
H 4	?	Cork	DBN - an old specimen, possibly of a later generation than the F1, with many seed set
?	179-	?	LIV - an anomalous specimen, which could be either a X viscidulus or a X londinensis segregate
37	1909	Dudley	Amphlett and Rea, 1910; Rep. Bot. Exch. Club (1909):415
6	1915	Shapwick	BIRM
17	1947	Frencham	Lousley, 1954 - two hybrids: one "closer to viscosus"
82	1959	Longniddry	LIVU - a few seeds set
16	1963	Sevenoaks	Proc. Bot. Soc. Brit. Is. (1964) 5:379

Note: As Lousley (1954) points out: this hybrid has frequently been found in Europe, and the major British herbaria all contain specimens from Central and North West Europe.

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